# PROVISIONING PATTERNS, DIET, AND REPRODUCTION OF MOUNTAIN BLUEBIRDS (*SIALIA CURRUCOIDES*) IN CLEARCUT VERSUS GRASSLAND HABITATS

A Thesis Submitted to the College of

Graduate and Postdoctoral Studies

In Partial Fulfillment of the Requirements

For the Degree of Master of Science

In the Department of Biology

University of Saskatchewan

Saskatoon

By

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## ABSTRACT

Clearcutting of forests results in early successional stages that resemble grasslands, and grassland birds such as mountain bluebirds (*Sialia currucoides*) may settle in these habitats during the breeding season. I had two main objectives in my study: 1) to determine if clearcuts are less productive habitats compared to grasslands regarding the amount and quality of prey; and 2) to test nestling gape size as a mechanism that limits parents' provisioning abilities.

Mountain bluebirds feed their nestlings prey such as larvae, spiders, and beetles. To determine what prey items parents were bringing, I placed microcameras in the nestboxes to film parental food deliveries. I found that parents in clearcuts brought larger, more nutritious prey than parents in grasslands but had a lower delivery rate. This lower delivery rate could indicate that prey was less abundant in clearcuts compared to grasslands, although arthropod abundance surveys need to be conducted to add confidence to this conclusion.

Adult bluebirds that settled in clearcuts did not differ in age or quality from those that settled in grasslands. Most reproductive parameters did not differ between habitats although fledglings in grasslands weighed more than fledglings in clearcuts. Clearcuts may be ecological traps based on foraging potential because bluebirds settled in both habitats equally but had nestlings of lower quality in clearcuts (potentially affecting the nestlings' chances at survival).

Finally, by observing parents feeding nestlings, I found that when parents brought larger prey items, they attempted to feed a nestling but withdrew the prey item from the nestling's gape more often than when offering smaller prey items. The smallest nestling of a brood was fed less often when parents brought large prey items. Patterns of prey allocation within broods were similar between clearcut and grassland habitats. Therefore, while prey volume and type differed between the two habitats, hatching asynchrony did not amplify these prey differences' effects on the swallowing ability of nestlings. In sum, clearcuts may be lower-quality habitats than grasslands, but settling in clearcut habitats may be a better alternative for mountain bluebirds compared to not breeding at all, if the availability of natural grassland habitats decreases.

## ACKNOWLEDGMENTS

I would like to thank Dr. Karen Wiebe for her guidance and support as my supervisor during this project. I would not have been able to do this without her. I would also like to thank my advisory committee members, Dr. Bob Clark and Dr. Christy Morrissey, for their insight during this project. I would also like to thank my external examiner, Dr. Erin Bayne, for his time and advice. Thank you to Dr. Lisha Berzins for her assistance and support during our spectrometer woes. Thank you to Stephen Srayko for his assistance with insect identification. I owe a lot to him and his insect books! I would also like to thank my sister, Jaclyn Morken, for proofreading this thesis and everything else I wrote throughout my university career.

I would like to thank the University of Saskatchewan and the Department of Biology for providing me with financial support. Thank you to all the friends I made here at the U of S, both during my undergraduate and graduate degrees for your advice and encouragement (especially Reid Bryshun). I would also like to thank my husband, Eric Stalwick, for his unwavering support during this project and for always believing in me. Finally, I would like to thank my family: Greg, Darci, Jaclyn, and Justin Morken, and Gary, Michelle, and Zoe Stalwick for their support and for listening to me talk about my thesis, whether it be about birds in general or the intricacies of statistics.

## DEDICATION

I would like to dedicate this thesis to my late grandmother, Lyla Blomquist. She passed away one week before I started my master's program. Lyla was extremely supportive of my biology career. She was always interested in the projects I was working on during my undergraduate degree and the research that I was doing during the summers. She was excited for me to start my master's program and I am sure she would have been interested in my results. My grandmother's encouragement was part of the reason that I pursued graduate studies.

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# CHAPTER 1: GENERAL INTRODUCTION

## 1.1 Habitat Selection

Selecting appropriate habitat is one of the most important decisions that an animal can make because it can influence reproductive output through mechanisms of predation risk or starvation. In some species, habitat selection may be innate or relatively fixed due to imprinting on cues from the natal habitat or from a habitat where they themselves raised a successful brood (Herlugson 1981; Bowers et al. 2014). Other species appear to use more flexible methods to select habitat based on signs of suitability. Whereas some animals can investigate a habitat and then decide that, for example, there is not enough food, and then move on to choose a different habitat, some animals are more time-restricted and need to decide quickly (Hollander et al. 2012). Migratory insectivorous birds are such animals, as they need to settle on their breeding grounds and often start breeding before the main food source emerges (Hildén 1965). Therefore, first-time breeders and birds that are not returning to their previous breeding site will rely on certain cues to indicate the suitability of a habitat and the future food availability (Hildén 1965; Schlaepfer et al. 2002; Kristan 2003). These cues may be based on vegetation structure or type such as tree height and ground cover (James 1971; Marshall and Cooper 2004; Moorman et al. 2012). However, not all individuals necessarily settle in an optimal habitat that provides enough food, breeding opportunities, and safety from predation.

There are several hypotheses for why some birds within a population settle in poor quality habitats. One explanation is territoriality and the model of "Ideal Despotic Distribution" which predicts that individuals will be forced to inhabit lower-quality habitats (sinks) if the higher-quality habitat is occupied (i.e., by dominant individuals) and this usually results in lower reproductive success in the poorer habitat type (Fretwell and Lucas 1969). According to this model, individuals forced into the lower-quality habitats are less competitive or of lower quality (small, young age, dull colour; Hildén 1965; Hollander et al. 2012), or they arrive later than the birds in the higher-quality habitat (Fretwell and Lucas 1969). Yet not all individuals that live in a lower-quality habitat may be forced there due to territoriality, but instead may either actively select or passively settle in an inferior habitat based on misleading cues.

Ecological traps are a special case of this maladaptive habitat choice that occurs when individuals do not avoid and may even actively prefer to inhabit an environment that lowers a component of fitness like survival or reproductive success (Donovan and Thompson 2001; Schlaepfer et al. 2002; Kristan 2003; Battin 2004). Ecological traps can occur in an altered environment when the bird bases its decision on a novel element in the environment (e.g. a man-made structure) which mimics a cue of a high-quality habitat in a natural situation (Schlaepfer et al. 2002). The birds' reduced fitness in the anthropogenic landscape means that ecological traps can be dangerous if the birds do not learn to adapt or change their preferences, potentially leading to the extinction of small populations (Schlaepfer et al. 2002; Battin 2004). The severity of the negative effect of an ecological trap (or attractive sink) on a population varies with the proportion of habitat available that is the ecological trap habitat (Delibes et al. 2001). Even a level of 30% of the habitat available being ecological traps can cause population size to decrease (Donovan and Thompson 2001) because productivity of individuals is reduced by choosing the poorer-quality habitat over the higher-quality habitat.

A clearcut is an area where most of the standing wood is removed, creating early successional habitat that may benefit grassland and shrubland birds (Vickery et al. 2005; Wallendorf et al. 2007). However, a previous study on mountain bluebirds (*Sialia currucoides*) proposed that clearcuts negatively affect them because predation rates were high in recent clearcuts and the bluebirds did not appear to consider the high predation risk when selecting their nesting site (Holt and Martin 1997). Studies of other bird species have generally recorded high nest predation rates along forest edges, especially for arboreal nests (Gates and Gysel 1978; Yahner and Scott 1989). The landscape edges created by clearcuts could be a problem for grassland birds that use that habitat. More specifically, De Santo and Willson (2001) reported that nest predation was high in clearcuts themselves, and Huhta and Jokimaki (2001) reported that clearcut-forest edges had higher nest predation than natural-forest edges. Therefore, clearcuts could be an ecological trap because they are structurally similar to grasslands but have a high predation risk. In contrast, Söderström and Karlsson (2011) found that corvids preyed on red-backed shrike (*Lanius collurio*) nests more often in grasslands rather than clearcuts in Sweden. However, these authors spoke only of corvid predators and may not have had mammalian predators in their study. Overall, many other studies seem to document higher

predation in clearcuts compared to grasslands, but the two habitats may differ in other ways that could affect the reproductive success of birds.

Clearcuts can influence key ecological processes and reduce the species richness usually found in an early successional ecosystem (Swanson et al. 2011). A clearcut usually has few snags for cavity-nesting birds (Edworthy and Martin 2013) and few perches for hunting (Swanson et al. 2011). However, if snags and standing dead trees are retained (according to some logging practices), there may be more perches and cavities available compared to grasslands (Conner and Adkisson 1974). Perches are important for hunters that scan for prey items in an open landscape (e.g. mountain bluebirds) because they reduce energy costs of foraging by reducing the need for energy-intensive hovering or flapping flight (Power 1980). Nevertheless, the increased predation risk in clearcuts could make clearcuts an unsuitable habitat and an ecological trap. While there are studies on the predation rates within clearcuts, there is very little information on how clearcuts affect foraging behaviour or the availability of prey for insectivorous grassland birds relative to their natural grassland habitats.

**1.2 Study Species and Field Site**

The mountain bluebird is a migratory, insectivorous cavity-nesting thrush weighing about 30 g. It is listed as a species of least concern (BirdLife International 2016). Although grasslands are their natural habitat (Power and Lombardo 1996), mountain bluebirds also settle in clearcut habitats. In Canada, the mountain bluebird breeding range extends from Manitoba through British Columbia and north into the Yukon Territory (Power and Lombardo 1996). Because mountain bluebirds willingly use nestboxes and their reproductive success does not vary between natural cavities and nestboxes (Holt and Martin 1997), they are easy to trap and use for experiments. Only females build the grass nest inside the box and incubate the clutch which varies from 3-8 eggs with an average of 5-6 eggs (Power and Lombardo 1996). Bluebirds forage in grassy areas for terrestrial arthropods (Erskine and McLaren 1976) and both parents bring whole food items to their nestlings, such as grasshoppers, beetles, caterpillars, and spiders (Power and Lombardo 1996).

During May and June of 2016 and 2017, I examined prey deliveries of mountain bluebirds and their effect on nestling growth and survival in two habitat types in central British Columbia: anthropogenically-altered clearcuts versus grasslands. Study sites containing open grassland habitats were established near Riske Creek (51°58’ N, 122° 31’ W, 986 m a.s.l.), 100

Mile House (51° 38' N, 121° 17' W, 970 m a.s.l.), and Bridge Lake (51° 28' N, 120° 43' W, 1140 m a.s.l.), with clearcut habitats also at the latter site (Figure 1.1). The multiple clearcuts were between 10-45 ha in size, 1-6 years old and were once mixed forests (including Douglas fir (*Pseudotsuga menziesii*), trembling aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), and white and hybrid spruce (*Picea glauca* and *P. glauca* X *engelmannii*)). The grazed grasslands had a native component of vegetation and often included small clumps of trees, mainly aspen and pine. Over 300 plywood nestboxes (16 x 16 x 30 cm with an entrance hole diameter of 4 cm) were placed in the field sites. Some clearcut nestboxes had metal sheets wrapped around the tree below them to protect them from squirrel and chipmunk depredation but subsequent analysis found no difference in predation rates between nestboxes with and without metal sheeting, so the treatment was not effective at reducing overall predation rates.

**1.3 Objectives**

The main objective of my thesis was to determine if the reproductive success of mountain bluebirds (*Sialia currucoides*) was negatively affected, via effects of lower food quality and quantity, by settling in clearcut habitats compared to their natural grassland habitat. To answer this question, I compared prey use and delivery rates of parents feeding their nestlings between the two habitats and looked for consequences on fledging success and other general reproductive parameters. Another main objective was to test nestling gape size as a mechanism that constrains the provisioning ability of parents and whether this results in an early death of the youngest nestling within an asynchronous brood. If prey diversity was lower in clearcuts with less suitable prey for small nestlings, I hypothesized that this might result in higher mortality rates for the youngest nestling in clearcut habitats.

In Chapter 2, I investigated whether prey types, prey sizes, and prey delivery rates to nestlings differed between mountain bluebird parents in clearcut and grassland habitats. If clearcuts were lower quality habitats I predicted that parents there would bring smaller, less nutritious prey types compared to grasslands. Furthermore, this should result in lower quality offspring in clearcuts compared to grasslands.

In Chapter 3, I examined the possibility of clearcuts being an ecological trap regarding prey availability. If clearcuts were an ecological trap, the mountain bluebird adults that settled there to breed should be of higher or similar quality to the adults in grasslands but the breeders in the clearcuts should have a lower reproductive output. To measure reproductive output, I

recorded parameters such as laying date, clutch size, egg size, and various measures of nestling quality. I also tested whether incubation patterns were different between the two habitats. If clearcuts lacked prey or had less nutritious prey, I predicted females will need to spend more time off the eggs to feed themselves, therefore, females in clearcuts would take more and longer recesses.

In Chapter 4, I determined if the size of prey affects the ability of parents to feed their nestlings, especially the smallest ones of asynchronous broods. I predicted that larger prey items with many appendages (e.g. large wings) would be more difficult for small nestlings to swallow. Therefore, if a habitat contained more prey types such as grasshoppers or moths compared to easily-swallowed larvae in the early stages of nestling development, younger nestlings would be more likely to die than their older siblings in that habitat.

**1.4 Thesis Format**

This thesis has been organized in manuscript format for publication. As a result, there may be some repetition of information throughout the text.

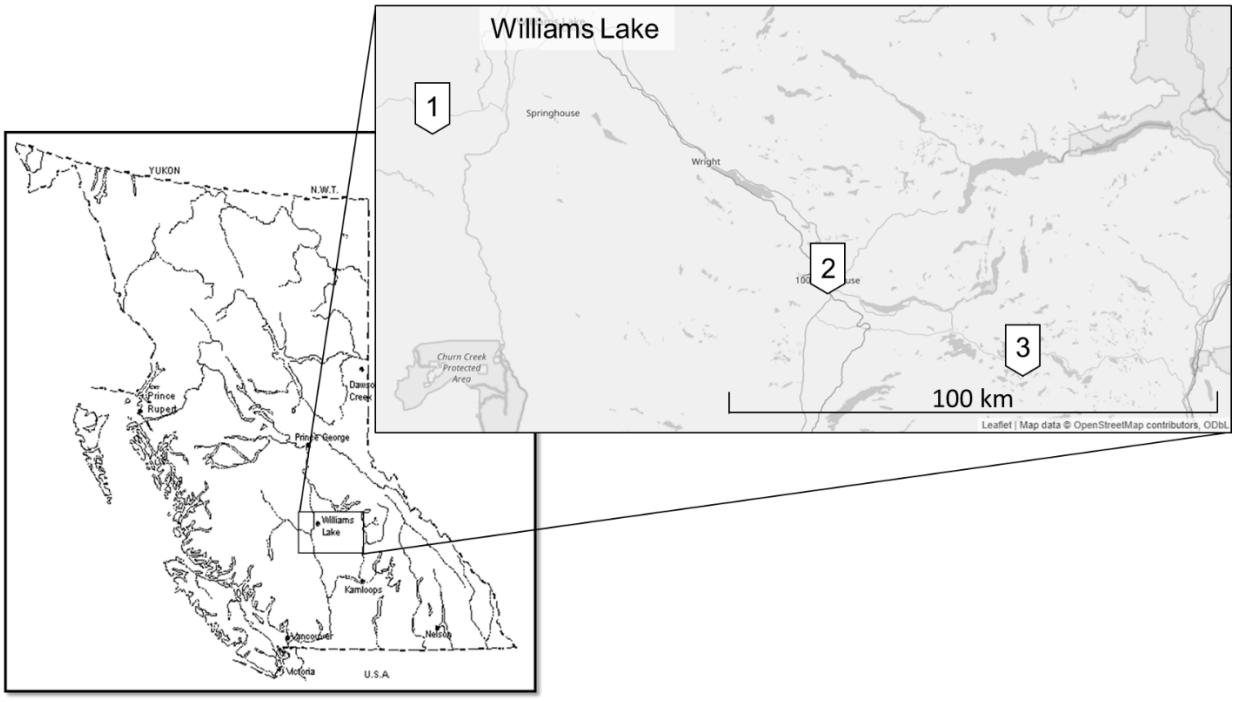


**Figure 1.1**. A map of the three study sites in central British Columbia, Canada. The box on the right is an enlarged map of the area within the box in the map of British Columbia on the left. The 1 indicates Riske Creek, the 2 is 100 Mile House, and the 3 is Bridge Lake. The grassland habitats are at all three sites and the clearcut habitats are around Bridge Lake.

# CHAPTER 2: PREY DELIVERY RATES AND PREY TYPES IN GRASSLAND AND CLEARCUT HABITATS

## 2.1 Introduction

For decades, forests in northern temperate regions have been subjected to logging practices that leave clearcuts on the landscape. Various species of birds that use early-successional or open habitats may settle in clearcuts and extensive research has focused on their reproductive success in these anthropogenically altered habitats. There are many studies on predation rates on nests in fragmented forest landscapes (e.g. Rudnicky and Hunter 1993; Holt and Martin 1997; De Santo and Willson 2001) but the species and structure of vegetation in clearcuts could also affect food supply for insectivorous birds (Ibbe et al. 2011; Highland et al. 2013). For example, compared to old forests, clearcuts in Sweden had more flowering plants, and as a result, more bumblebees and butterflies (Korpela et al. 2015). Whereas open clearcuts may superficially resemble natural grasslands, the two habitats may contain different forb or shrub species and hence different types of arthropod prey. Grasslands in Sweden had a greater diversity but a lower abundance of butterfly species than clearcuts (Jonason et al. 2010) and Highland et al. (2013) found that moth diversity and abundance was lowest in clearcuts compared to other natural openings such as meadows.

Previous studies comparing clearcuts and grasslands have focused on specific arthropods, and to my knowledge, there is no information regarding dietary differences of insectivorous birds using these different habitats. Here, I did not attempt to measure prey availability but instead focused on what mountain bluebird (*Sialia currucoides)* parents delivered to their nestlings (prey use). Lepidopteran larvae feature prominently in the diet of many species of passerine nestlings (Skipper and Kim 2013; Wiebe and Slagsvold 2015; Serrano-Davies and Sanz 2017) including bluebirds (Pinkowski 1978; Power 1980). Larvae, lacking the long appendages and hard unpalatable chitinous exoskeleton (Finke 2007) of other insects such as grasshoppers, are often relatively easy to swallow (Herlugson 1982; Bańbura et al. 1999). Several studies have documented that parents feed mostly soft prey such as larvae and spiders in the early stage of the nestling period (Bańbura et al. 1994; Wiebe and Slagsvold 2009), and later

may include or switch to larger insects such as grasshoppers and beetles to cope with increased food demands of older nestlings (Pinkowski 1978; Wiebe and Slagsvold 2014).

Nutritional quality of arthropod prey is very important in nestling development. Orthoptera adults and Lepidoptera larvae have a high protein content (Bukkens 1997, Barker et al. 1998), and larvae of Lepidoptera and Coleoptera are high in fat and calorie-rich (Barker et al. 1998). Not all larvae are the same nutritionally, but they are important prey items for nestlings in general. Donald et al. (2001) reported higher nestling body conditions in skylarks (*Alauda arvensis*) when parents fed the nestlings more insect larvae. The mass of blue tit (*Cyanistes caeruleus*) nestlings also increased as the proportion of larvae in their diet reached 65%-75%, after which nestling mass started to decrease (García-Navas et al. 2013). Spiders are also believed to be favoured prey for young insectivorous nestlings. Spiders contain an important amino acid called taurine that may aid in the brain development of young nestlings (Ramsay and Houston 2003; Arnold et al. 2007), and spiders have a higher protein content than larvae (Ramsay and Houston 2003) and adult Coleoptera (Razeng and Watson 2015). Blue tit nestlings that were fed spiders had a higher body condition than those lacking spiders in their diet (Serrano-Davies and Sanz 2017). García-Navas et al. (2013) found that blue and great tit (*Parus major*) nestlings that were 10 days (d) old and had a diet rich in spiders had relatively long tarsi, perhaps because the high calcium content in spiders (Graveland and Van Gijzen 1994) could increase the rate of skeletal mineralization (Tilgar et al. 2005). Therefore, it seems that larvae and spiders are the "best" terrestrial prey for insectivorous, passerine nestlings based on both nutrition and ease of swallowing, although grasshoppers, which are high in protein, could be important as the nestlings grow and require larger prey to keep up with their increasing caloric demand.

In addition to prey type and size, delivery rates to nestlings will affect their growth. Experimental enlargements of brood size have shown that parents of many birds increase delivery rate to nestlings, presumably in response to higher brood demands and begging cues from nestlings (Siefferman and Hill 2007; Musgrove and Wiebe 2014). However, high delivery rates can be associated with a decrease in prey item quality if parents spend less time searching for high-quality prey (Wright et al. 1998; García-Navas and Sanz 2010; Wiebe and Slagsvold 2015). Other features intrinsic to the parent, such as its age and quality, might also influence foraging skill (Desrochers 1992; Hidalgo-Garcia 2006; Daunt et al. 2007) and hence delivery

rates to nestlings. Physical characteristics of the habitat itself might also influence hunting success or effort. For example, perches can reduce the energy required for foraging by birds that hunt by a sit-and-scan method, such as bluebirds (Power 1980).

Here, I compare delivery rates, prey types, and prey volumes ($mm^3$) brought by male and female mountain bluebirds to nestlings in clearcut and grassland habitats. I assumed that larvae and spiders were the most nutritious prey items (especially for small nestlings) and that large prey would be progressively favoured over small prey as the nestlings grew. If clearcuts are lower-quality habitats for foraging, I predicted that either 1) prey quality would be similar between habitats but delivery rates (prey quantity) lower in clearcuts if prey were less abundant there; or 2) prey quality would be lower in clearcuts and delivery rates would be the same or higher than in grasslands if parents try to compensate. Regarding parental traits, I predicted that older (experienced) parents with higher body conditions and brighter, bluer feathers would deliver prey items at a higher rate than lower-quality parents in both habitats, but that the differences in nestling feeding between high- and low-quality parents would be more obvious in clearcut habitats. Finally, I compared delivery rates with the number of perches in the habitat type, predicting that perches would make hunting more efficient and lead to greater delivery rates.

## 2.2 Methods

### *2.2.1 Study Site and Study Species*

I studied mountain bluebirds at three study sites in central British Columbia during the breeding season of 2016 and 2017: two grassland areas and one mainly clearcut area. The grassland sites were Riske Creek (51°58’ N, 122° 31’ W, 986 m a.s.l.) and 100 Mile House (51° 38' N, 121° 17' W, 970 m a.s.l.). There were both grassland and clearcut sites at Bridge Lake (51° 28' N, 120° 43' W, 1140 m a.s.l.). Over 300 plywood nestboxes were placed on retained trees in logging cuts that were between 10-45 ha and 1-6 years post-harvest, and on fenceposts in grazed grasslands that contained a mix of native and introduced grasses and forbs. All boxes were at least 400 m apart. The clearcuts were originally mixed forests that included Douglas fir (*Pseudotsuga menziesii*), trembling aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), and white and hybrid spruce (*Picea glauca* and *P. glauca* X *engelmannii*).

The mountain bluebird is a migratory, insectivorous cavity-nesting thrush that may settle in clearcuts (Holt and Martin 1997) despite its natural habitat being grasslands. Mountain

bluebirds begin to settle on the study area around mid-April after migration, and lay clutches of 5-6 eggs on average (Power and Lombardo 1996) in May. Only the female incubates, but both sexes provision the offspring with a variety of invertebrate prey, including Lepidoptera (adults and larvae), Arachnida, Coleoptera, Orthoptera, Hymenoptera, and sometimes Annelida (Pinkowski 1978; Power 1980; Herlugson 1982). The nestling period lasts between 15-22 days (Johnson et al. 2013a).

*2.2.2 Field Work*

After nestlings hatched, adults were captured using swing-door traps over the entrance hole to the box and banded with a unique set of aluminum and plastic colour bands. The birds were weighed, and six structural body-size variables were taken: head-bill length, 9th primary length, central rectrix length, tarsus length, culmen length and flattened wing chord. I calculated a single size variable using these six measurements in a principal component analysis separated by sex (Rising and Somers 1989). All size variables loaded positively on the first axis (PCA1), and I calculated a body condition index as the residual of a regression of body mass on PCA1 (Labocha and Hayes 2012; Wiebe and Vitousek 2015). Birds were aged as adults versus yearlings based on molt (Pyle 1997). Finally, I took the left wing secondary feather S2 for analysis of colour in the lab.

I analyzed feather colour with an Ocean Optics Flame Miniature Spectrometer and a DH-mini UV-VIS deuterium halogen light source with the integration time set to 325 ms, the average scans to 2, and the boxcar to 10. For each feather, I took three readings that were 2.5 cm from the tip of the feather on the leading edge of the vein. I used the R library "pavo" (Maia et al. 2013) to obtain the variables of brightness, chroma, and hue (Montgomerie 2006; Berzins and Dawson 2016). There were two chroma variables, one for the UV range (300-400 nm) and one for the visible spectrum in the blue range (400-512 nm), which indicated the relative proportion of light reflected by the feather in their respective ranges relative to the entire spectrum. Brightness was the average amount of light reflected by the feather (% reflected) on the spectrum within 300-700 nm. Finally, hue was the wavelength of the maximum reflectance of the feather. Principal components analyses of all four of these variables determined that chroma did not vary greatly between individuals, and therefore I did not use these variables in my analyses. Brightness and hue were not correlated so I used them as separate variables.

On the day of filming, I weighed the nestlings at each box and then placed micro-cameras (either custom-built motion-triggered digital mini cameras or GOPROs) in the ceiling of each nestbox to film parental deliveries and identify the taxa and size of prey delivered during 3-hour filming blocks. This length of filming was sufficient to record 1 - 90 (mean 26) deliveries by parents. I did not start calculating delivery rates (deliveries/hour) until the first visit of a parent to the nest, indicating acclimatization to the camera. The size of the prey was calculated by comparing the prey item to the bill of the adult, which was of known size, and using the equation of a cylinder: $\pi * (0.5\text{width})^2 *$ length to calculate the volume of the body of insect prey (excluding wings and legs; Slagsvold and Wiebe 2007). I filmed at 26 clearcut boxes and 25 grassland boxes in 2016, and at 25 clearcut boxes and 16 grassland boxes in 2017. The intent was to film at three nestling stages: early (0-4 d old), middle (5-11 d old) and late ($\geq$12 d old) at each box, but cold weather prevented a few filming sessions (see Table 2.1 for sample sizes). Regardless of filming, I weighed nestlings at 100 boxes in the early stage, 101 boxes in the middle stage, and 114 boxes in the late stage in total between the two years and habitats.

I also sampled the vegetation and habitat structure on each bluebird territory. Bluebird territories can be greater than 5 ha (Power and Lombardo 1996). Therefore, the territories were too large to sample completely so for an index of the number of perches in the locality of the nestbox, I counted: 1) "fencepole-height" structures 1.5-3 m tall within 50 m of the box; 2) perches $\geq$ 3 m tall (e.g. trees) within 100 m of the box; and 3) perches and bushes that were 0.5-1.5 m tall encountered while walking four 50-metre transects in cardinal directions from the box. Additionally, I sampled vegetation cover (species of forbs and % cover) within two 1 $m^2$ plots placed 25 m from the focal nestbox (see Appendix 1 for vegetation variables).

*2.2.3 Statistical Analyses*

I used R version 3.4.3 (R Core Team 2017) and report data as means $\pm$ standard error in the results section, unless indicated otherwise. To analyze prey volume, I used a linear mixed effects model (library "lmerTest", Kuznetsova et al. 2017) with habitat type (grassland vs. clearcut), parent sex, nestling stage (early, mid, late), brood size, and year as fixed effects. The random effects were date and nestbox, and the dependent variable, prey volume, was log-transformed for a normal distribution. Pairwise interactions were included in initial models throughout this chapter but deleted if not significant, and main effects that were not significant ($\alpha > 0.05$) were sequentially deleted to simplify models although habitat was always retained as the

main hypothesis of interest. The models' remaining explanatory variables are in Table 2.2, 2.3, and 2.4. Another set of LMMs was used to determine if parental characteristics (size, body condition, age, feather brightness, and feather hue) were associated with the size of prey delivered. These models (one for each parent) included habitat type, nestling stage, year, and each parental characteristic as fixed effects, and date and nestbox as random effects. I used the command "difflsmeans" to determine if there were any statistical differences in prey volume between nestling stages.

To analyze the taxon of prey delivered, I used generalized linear mixed effects models with a binomial distribution (library "lmerTest", Kuznetsova et al. 2017). The prey categories were: larvae, Coleoptera adults, spiders, Orthoptera, Lepidoptera adults, and Hymenoptera combined with Diptera. The latter two prey were combined because there were relatively few of each and the taxa structurally and nutritionally resembled each other. Fixed factors included habitat type, brood size, nestling stage, sex of parent, and year, and random factors were date and nestbox. I used library "multcomp" (Hothorn et al. 2008) to perform a post-hoc Tukey test when needed to determine the potential significant differences in a factor with more than two groups for GLMMs. To obtain *P*-values for GLMMs, I used the R library "car" and the function "Anova" (Fox and Weisberg 2011).

LMMs for delivery rate (parents combined) included nestbox as a random variable, and habitat type, brood size, nestling stage, parent sex, fencepole-height perch density, taller perch density (e.g. trees), and year as fixed factors. Since shrub density was strongly related to habitat type, I did not enter shrubs as a separate variable in models with habitat. Subsequent models with the same fixed effects were run for the sexes individually, and those models also included traits of the individual such as age, condition, and colour. I used t-tests to compare the availability of perches between grassland and clearcut habitat types directly.

I ran three LMMs for nestling mass, one for each nestling stage (early, middle, and late). The early and middle nestling stage models included habitat and year as the fixed effects and age and nestbox as random effects. By the late stage, nestlings could be sexed by plumage colour and so that model included habitat, nestling sex, and year as fixed effects and nestbox as a random effect.

## 2.3 Results

The diversity of forb taxa appeared higher in clearcuts although many plant species occurred in both habitats. Clearcuts had less grass cover than grasslands (16% vs 34%) and tended to have more dead wood and less bare ground than grasslands (Appendix 1). Besides grass species, the main plant family in grasslands was Asteraceae and the main plant family in clearcuts was Rosaceae. In terms of habitat structure, there were more perches 1.5-3 m tall in clearcuts than grasslands ($t_{45}$=4.67, $P$<0.001; Figure 2.1), but perches taller than 3 m (such as trees) were not more numerous in clearcuts ($t_{84}$=1.60, $P$=0.113). Lastly, the density of perches shorter than 1.5 m (e.g. shrubs) was greater in clearcuts than grasslands ($t_{61}$=11.55, $P$<0.001).

### *2.3.1 Prey Volume*

Adults in clearcuts on average brought larger prey (322 $mm^3$ $\pm$ 6.8) than those in grasslands (297 $mm^3$ $\pm$ 6.1), and males brought larger prey to their nestlings than females (Figure 2.2). Prey volume also increased with nestling stage, with birds bringing larger prey in the middle and late stages compared to the early stage (Table 2.2). There were no significant interactions in the model although when separated by sex, habitat was no longer significant among males, but the stage of nestling period was still important (Figure 2.2). None of the males' traits were associated with prey volume. Among females, the effect of habitat was still significant, as was nestling stage (Figure 2.2), and of the individual traits only body size was significant, with larger females bringing larger prey.

### *2.3.2 Prey Type*

Sex of the parent did not affect the proportion of larva prey brought to the nestlings, but there was a habitat and nestling stage interaction regarding larva proportion (Table 2.3; Figure 2.3). Adults in clearcuts but not grasslands increased the proportion of larvae with nestling stage, and overall, parents in clearcuts brought more larvae at the middle and late stages compared to grasslands. The proportion of the other nutritious prey type, spiders, was also higher in clearcuts than in grasslands (Table 2.3; Figure 2.3). However, adults in both habitats brought significantly more spiders in the early stage of nestling growth than the middle and late stages.

For Coleoptera adults (beetles), there was a habitat and nestling stage interaction (Table 2.3; Figure 2.3). The proportion of the deliveries that were beetles increased during the middle nestling stage in grasslands but did not increase in clearcuts until the late stage, and more beetles were delivered in grasslands during the middle and late stage compared to clearcuts. There was

also an interaction between habitat and sex on Coleoptera proportions. Males in grasslands brought more beetles than females, and adults in grasslands in general brought more beetles than their counterparts in clearcuts. The use of the final three prey groups: Orthoptera, Lepidoptera, and the combined Hymenoptera and Diptera was not associated with either sex of the parent or habitat type (Table 2.3). Appendix 2 contains all prey types found in both habitats.

*2.3.3 Delivery Rates*

The delivery rate of prey to nestlings was higher in grasslands (12.4 $\pm$ 0.6 prey/hour) than in clearcuts (9.9 $\pm$ 0.4 prey/hour; Table 2.4). Delivery rate also increased with brood size. There was a significant interaction between nestling stage and parent sex, where males had a higher delivery rate than females in the early nestling stage when females spent time brooding ($F_{1,68}$=5.58, $P$=0.021) and a lower delivery rate than females in the late nestling stage ($F_{1,30}$=27.38, $P$<0.001; Figure 2.4). Males and females had similar delivery rates in the middle nestling stage ($F_{1,93}$=3.28, $P$=0.07). Females increased their delivery rates after the early nestling stage ($F_{2,126}$=9.39, $P$<0.001) while males did not significantly change their delivery rates as nestlings aged ($F_{2,136}$=2.44, $P$=0.09).

When the delivery rates of the sexes were considered independently, males increased deliveries with increasing brood size and deliveries were greater in grassland than in clearcut habitats (Table 2.4). There was a male condition and feather hue interaction. Males with a lower hue (bluer) had delivery rates that decreased with increasing male condition, whereas the delivery rate of less blue males (higher hues) did not vary with their body condition. Also, males of low body condition had higher delivery rates if they were bluer, although this pattern diminished as body condition increased. The delivery rate of females significantly increased with nestling stage (Table 2.4; Figure 2.4) and was affected by a habitat and brood size interaction. Delivery rates increased with brood size in grasslands but not in clearcuts. No attributes of the female (age, condition or colour) were significant predictors of delivery rates.

*2.3.4 Nestling masses*

Nestlings weighed 6.9 g $\pm$ 0.1 in the early nestling stage in both habitats ($F_{1,90}$=0.96, $P$=0.33) and 21.3 g $\pm$ 0.3 in the middle nestling stage in both habitats ($F_{1,96}$=0.49, $P$=0.49). For mass near the time of fledging when nestling sex could be determined, another model indicated that male nestlings at the late stage weighed more than females ($F_{1,425}$=14.53, $P$<0.001) and the

mass of these older nestlings was higher in grasslands than in clearcuts ($F_{1,84}$=6.75, $P$=0.011; Figure 2.5). There was no significant interaction between sex and habitat on fledgling mass.

## 2.4 Discussion

The prey deliveries of bluebirds to their nestlings differed in some respects between clearcut and grassland habitats, but the patterns did not clearly conform to either of my predictions because the quality of prey types (proportion of larvae and spiders) was higher in clearcuts but provisioning rates and fledgling mass were lower in clearcuts than in grasslands. This suggests that clearcuts may provide less food for bluebirds overall, although there were conflicting patterns with different aspects of provisioning: prey volume, prey type and abundance.

### *2.4.1 Prey Volume*

Bluebird parents of both sexes brought larger prey as nestlings grew older. This pattern makes sense because small nestlings cannot physically swallow large items, but older nestlings have higher energy demands so parents switch to large prey for older nestlings (Slagsvold and Wiebe 2007). Similarly, other passerine birds demonstrate the pattern of increasing their prey size or overall biomass as their nestlings age (Adler and Ritchison 2011; Wiebe and Slagsvold 2014). I also found that males brought larger prey on average than females, similar to some other passerines such as pied flycatchers (*Ficedula hypoleuca*) and blue tits (Bańbura et al. 2001; Wiebe and Slagsvold 2014). Females are usually more attuned to the needs of their nestlings (Budden and Beissinger 2009; García-Navas et al. 2014; Liu et al. 2014) and may therefore bring smaller prey suitable for young nestlings to ensure they get sufficient food. Alternatively, they may not be intentionally searching for small prey but only bring it because they may be spending more time looking after the nestlings in the box (i.e. brooding) than males and may have less time to find larger prey (Wiebe and Slagsvold 2009). I also found that larger females (but not larger males) brought larger items than smaller individuals of the same sex, possibly because a larger bill made handling larger prey easier.

Overall, adults in clearcuts brought larger prey items than adults in grasslands, although when the data were analyzed by sex, the pattern was driven by the female, since the size of the male's prey did not vary according to habitat type. On the surface, it appears the larger average size of prey in clearcuts indicates that foraging is more profitable there if nestlings could be satiated without needing to increase delivery rates. However, if the range of prey volumes was

greater in the grasslands, the females there might have been targeting smaller items for the small nestlings, which might have increased the survival of small nestlings in asynchronous broods (see Chapter 4).

*2.4.2 Prey Type*

Larvae were an important prey category in all nestling stages in both habitats, comprising 34% of all prey items recorded, but the proportion increased in the middle and late stages in clearcuts, suggesting that larvae became more common in that habitat as the summer progressed. However, direct sampling of prey in each habitat is needed to confirm differences in abundance in the environment. Few studies have examined insect biodiversity and abundance in clearcuts compared to grasslands, so patterns are difficult to generalize. There were more butterflies in clearcut habitats compared to grasslands in Sweden (Jonason et a. 2010) but fewer moths in clearcuts in Oregon, USA (Highland et al. 2013), so the overall effect of anthropogenic disturbance on the abundance of Lepidopteran larvae is unclear. In clearcuts, the increase in larvae in the diet over time was accompanied by a decrease in spiders. Similarly, blue tits bring fewer spiders as their nestlings grow (García-Navas et al. 2012). Overall, adults in clearcuts brought a larger proportion of spiders to offspring compared to grasslands. Assuming that larvae and spiders are the highest quality food items, clearcuts appear to contain a greater proportion of high-quality prey than grasslands, or at least adults in clearcuts bring more high-quality prey than adults in grasslands.

As the proportion of spiders in the diet declined as young nestlings grew, adults in clearcuts brought proportionately more larvae whereas those in grasslands brought more beetles (Coleoptera) during the middle and late stages. It is unknown if the shift to Coleoptera or larvae from spiders in the two habitats was driven by choice or shifting seasonal availability of prey. Regardless, adult Coleoptera appear to be less nutritious and digestible than larvae, but the diversity of insects appears to be higher in the grassland diet (see Appendix 2), so perhaps such alternate prey was abundant in grasslands and energetically cheap to hunt. Wood warblers (*Phylloscopus sibilatrix*) also brought more spiders early in the nestling period and switched to more winged insects as nestlings got older (Maziarz and Wesolowski 2010), which may provide efficient energy for older nestlings.

The other three main groups of prey did not differ between clearcuts and grasslands (Orthoptera, Lepidoptera adults, and the combined Hymenoptera and Diptera group), being quite

uncommon in the diet, although grasshoppers are an important food source for bluebirds elsewhere (Pinkowski 1978; Power 1980; Herlugson 1982). At the relatively high latitude of my study sites, grasshoppers did not seem to emerge in sizable numbers until after the nestling stage (July), and Pinkowski (1978) also reported that grasshoppers became more common in the diet of eastern bluebird (*Sialia sialis*) nestlings in late summer. Previous studies on mountain bluebirds have not found that male and female parents deliver different species of prey to nestlings (Power 1980). My results suggested that males in grasslands brought more beetles than females in grasslands, which suggests females might have focused on obtaining higher-quality prey for nestlings, but this difference was not apparent in clearcuts or regarding any other prey types, so sexual differences in prey choice seem small.

*2.4.3 Delivery Rates*

Adults in grasslands had higher delivery rates than those in clearcuts, which suggests that prey were more abundant or easier to find in grasslands. Therefore, although the adults in clearcuts fed their nestlings a higher proportion of nutritious prey items (larvae and spiders), they were not feeding them as often as adults in grasslands probably because prey was scarcer in clearcuts. Conversely, since adults in clearcuts were bringing larger, more nutritious prey items, perhaps there was a prey volume/nutrition vs. delivery rate trade-off (Kadin et al. 2016), as was found in European starlings (*Sturnus vulgaris*; Wright et al. 1998) and titmice (Wiebe and Slagsvold 2015). Fledgling mass would also indicate if the parents were able to bring enough food. Nestling mass was similar between habitats in the early and middle nestling stage but fledglings in grasslands were heavier than fledglings in clearcuts. Therefore, as nestlings grew and required more food, parents in clearcuts were not able to feed their nestlings as much as those in grasslands, resulting in fledglings of lower mass compared to fledglings in grasslands.

As might be expected with the increased demand, delivery rate increased with brood size, which is the same pattern found in many studies of insectivorous passerines such as blue tits (Stauss et al. 2005; García-Navas and Sanz 2010) and grasshopper sparrows (*Ammodramus savannarum*; Adler and Ritchison 2011). With respect to sex differences in provisioning rates, I found that females provisioned less than males at the youngest nestling stage but more than males at the oldest stage. Other studies of mountain bluebirds have reported that females feed the nestlings more often than the males later in the nestling period, although males may have the same or higher feeding rates during the early nestling period when females brood (Power 1980;

Balenger et al. 2007). Perhaps males in my study slightly decreased the amount of work with older nestlings because the females were increasing their delivery rates. Pinkowski (1978) also reported that eastern bluebird males decreased their delivery rate later in the nestling period. This decrease in delivery rate in my study might have been related to the fact that males were bringing larger food than females overall, similar to a pattern where great reed warblers (*Acrocephalus arundinaceus*) had lower delivery rates with increased prey load sizes (Sejberg et al. 2000).

No female characteristics were correlated with the delivery rate of females, but there was an interaction between male body condition and male feather hue on the delivery rate of males. Among males with a lower body condition, less-blue males had a lower delivery rate than bluer (higher-quality) individuals. However, among males with higher body condition, bluer males had lower delivery rates. Highly ornamented males in good condition may obtain the territories with the best quality prey and hence need to provision less, as was the case in yellow warblers (*Setophaga petechia*; Studd and Robertson 1985). Alternatively, highly ornamented males in good condition might invest less in the current brood to court other females and secure extra-pair mates (Crary and Rodewald 2012). Mountain bluebirds are not always monogamous and may have extrapair fertilizations (Balenger et al. 2009), and brighter, bluer mountain bluebirds are more likely to engage in extrapair fertilizations (O'Brien and Dawson 2011), so perhaps the bluer males in my study, when they were in good condition, invested more in extra-pair mating effort rather than provisioning for the current brood.

*2.4.4 Effects of Habitat Structure*

There were more shrubs in clearcut habitat and there was a lower delivery rate in clearcuts. Bluebirds appear to prefer short and sparse vegetation for foraging, either because shrubs obscure the ground and make it harder to see and reach prey items, or because shrubs make it more difficult for bluebirds to detect predators (Power 1980). Trees and shorter perches such as fencepole-height perches are used by insectivorous birds to forage (Power 1980; Robertson 2012). Clearcuts had more fencepole-height perches (mostly large bushes and saplings) and more shrubs than grasslands (see Figure 2.1), but such perches were not sufficient to cause high delivery rates in clearcuts and the shrub density might have hindered foraging.

In sum, the diet of nestling bluebirds in clearcuts seems to indicate that the habitat contains larger, more nutritious prey than grasslands, but that the abundance of prey items may be lower. Future studies should measure the abundance of arthropod species in these habitats to

determine what is available and to what degree birds are actively selecting food types. The effect of individual traits such as age, body condition, or plumage hue on provisioning patterns were not expressed in one habitat type more than the other, indicating perhaps that energetic stresses did not push birds to their provisioning limit or else high-quality birds with sufficient resources invested in alternate reproductive opportunities. Fledgling body masses were lower in clearcuts, suggesting that parental provisioning was less efficient in the anthropogenically created habitat.

**Table 2.1.** Sample sizes of mountain bluebird broods filmed in two habitat types in central British Columbia and at three nestling stages (early: 0-4 d; middle: 5-11 d, late ≥ 12 d).

| **Year** | **Grassland** | | | **Clearcut** | | |
|---|---|---|---|---|---|---|
| | Early | Middle | Late | Early | Middle | Late |
| **2016** | 13 | 18 | 7 | 12 | 18 | 4 |
| **2017** | 13 | 17 | 9 | 25 | 22 | 8 |

**Table 2.2.** Linear mixed effects models for prey volume ($mm^3$) brought by mountain bluebirds nesting in either grassland or clearcut habitats in central British Columbia. The first model is for overall prey volume with both parents pooled and then the models were separated by the sex of parents to incorporate morphological measures of the individuals as explanatory variables. Significant *P*-values are bolded.

| Dependent Variable | Model | Coefficient[1] ± SE | DF | *F* | *P* |
|---|---|---|---|---|---|
| Prey Volume | | | | | |
| | Habitat Type | -0.18 ± 0.08 (grass) | 1,130 | 6.11 | **0.015** |
| | Parent Sex | 0.10 ± 0.03 (male) | 1,4798 | 11.14 | **<0.001** |
| | Nestling Stage | 0.62 ± 0.08 (middle)<br>0.66 ± 0.10 (late) | 2,157 | 39.46 | **<0.001** |
| | Year | 0.17 ± 0.07 (2017) | 1,151 | 6.34 | **0.013** |
| Male's Prey Volume | | | | | |
| | Habitat Type | -0.11 ± 0.09 (grass) | 1,124 | 1.55 | 0.22 |
| | Nestling Stage | 0.64 ± 0.10 (middle)<br>0.67 ± 0.13 (late) | 2,153 | 26.04 | **<0.001** |
| | Year | 0.19 ± 0.09 (2017) | 1,143 | 4.59 | **0.034** |
| Female's Prey Volume | | | | | |
| | Habitat Type | -0.21 ± 0.08 (grass) | 1,90 | 6.05 | **0.016** |
| | Nestling Stage | 0.65 ± 0.09 (middle)<br>0.71 ± 0.12 (late) | 2,120 | 30.14 | **<0.001** |
| | Female Size | 0.11 ± 0.04 | 1,148 | 6.44 | **0.012** |
| | Year | 0.11 ± 0.08 (2017) | 1,130 | 1.85 | 0.18 |

**1** Each variable's coefficient estimates (unstandardized) were obtained using the "summary" function in R and the degrees of freedom, F, and *P*-values were obtained using the "anova" function. For categorical variables, the coefficient is calculated for the category in parentheses to compare to the intercept (the category of the variable not indicated in parentheses), but the other columns refer to the categorical variable as a whole.

**Table 2.3.** GLMMs for prey types (proportion) brought by mountain bluebirds nesting in either grassland or clearcut habitats in central British Columbia. Significant *P*-values are bolded.

| Dependent Variable | Model | Coefficient[1] ± SE | DF | $\chi^2$ | *P* |
|---|---|---|---|---|---|
| Larva | | | | | |
| | Habitat Type | -0.13 ± 0.22 (grass) | 1 | 17.63 | **<0.001** |
| | Nestling Stage | 0.73 ± 0.20 (middle)<br>0.63 ± 0.27 (late) | 2 | 7.72 | **0.021** |
| | Parent Sex | -0.07 ± 0.07 (male) | 1 | 1.05 | 0.31 |
| | Year | 0.04 ± 0.13 (2017) | 1 | 0.11 | 0.74 |
| | Habitat Type * Nestling Stage | -0.72 ± 0.29 (grass & middle)<br>-0.74 ± 0.38 (grass & late) | 2 | 7.06 | **0.029** |
| Spider | | | | | |
| | Habitat Type | -0.53 ± 0.14 (grass) | 1 | 13.72 | **<0.001** |
| | Nestling Stage | -1.03 ± 0.15 (middle)<br>-1.30 ± 0.21 (late) | 2 | 60.42 | **<0.001** |
| | Year | 0.28 ± 0.14 (2017) | 1 | 3.77 | 0.052 |
| Coleoptera | | | | | |
| | Habitat Type | -0.15 ± 0.32 (grass) | 1 | 12.89 | **<0.001** |
| | Nestling Stage | 0.42 ± 0.24 (middle)<br>0.80 ± 0.31 (late) | 2 | 63.89 | **<0.001** |
| | Parent Sex | -0.01 ± 0.15 (male) | 1 | 12.36 | **<0.001** |
| | Year | -0.04 ± 0.17 (2017) | 1 | 0.07 | 0.79 |
| | Habitat Type * Nestling Stage | 1.16 ± 0.31 (grass & middle)<br>1.29 ± 0.40 (grass & late) | 2 | 15.93 | **<0.001** |
| | Habitat Type * Parent Sex | 0.45 ± 0.18 (grass & male) | 1 | 5.90 | **0.015** |
| Orthoptera | | | | | |
| | Habitat Type | 0.48 ± 0.32 (grass) | 1 | 2.31 | 0.13 |
| | Parent Sex | -0.22 ± 0.14 (male) | 1 | 2.31 | 0.13 |
| | Year | -0.40 ± 0.29 (2017) | 1 | 1.98 | 0.16 |

| Dependent Variable | Model | Coefficient[1] ± SE | DF | $\chi^2$ | *P* |
|---|---|---|---|---|---|
| Lepidoptera | | | | | |
| | Habitat Type | -0.21 ± 0.21 (grass) | 1 | 1.09 | 0.30 |
| | Parent Sex | 0.22 ± 0.17 (male) | 1 | 1.59 | 0.21 |
| | Year | -0.54 ± 0.21 (2017) | 1 | 6.71 | **0.010** |
| Hymenoptera + Diptera | | | | | |
| | Habitat Type | 0.006 ± 0.20 (grass) | 1 | 0.001 | 0.98 |
| | Parent Sex | 0.23 ± 0.12 (male) | 1 | 3.60 | 0.06 |
| | Year | -0.54 ± 0.20 (2017) | 1 | 7.61 | **0.006** |

**1** Each variable's coefficient estimates (unstandardized) were obtained using the "summary" function in R and the degrees of freedom, $\chi^2$, and *P*-values were obtained using the "Anova" function. For categorical variables, the coefficient is calculated for the category in parentheses to compare to the intercept (the category of the variable not indicated in parentheses), but the other columns refer to the categorical variable as a whole.

**Table 2.4.** LMMs for delivery rates (prey deliveries/hour) to nestlings by mountain bluebirds in grassland or clearcut habitats in central British Columbia. There is an overall delivery rate with both parents and then the models were separated by sex. Significant *P*-values are bolded.

| Dependent Variable | Model | Coefficient[1] ± SE | DF | *F* | *P* |
|---|---|---|---|---|---|
| Overall Delivery Rate (DR) | | | | | |
| | Habitat Type | 1.56 ± 0.38 (grass) | 1,55 | 16.74 | **<0.001** |
| | Brood Size | 1.00 ± 0.18 | 1,102 | 31.10 | **<0.001** |
| | Nestling Stage | 1.74 ± 0.50 (middle)<br>3.05 ± 0.70 (late) | 2,316 | 2.34 | 0.10 |
| | Parent Sex | 1.18 ± 0.52 (male) | 1,249 | 7.58 | **0.006** |
| | Year | -0.25 ± 0.35 (2017) | 1,184 | 0.49 | 0.49 |
| | Nestling Stage * Parent Sex | -2.15 ± 0.71 (middle & male)<br>-4.34 ± 0.96 (late & male) | 2,249 | 11.04 | **<0.001** |
| Male DR | | | | | |
| | Habitat | 1.55 ± 0.67 (grass) | 1,47 | 5.36 | **0.025** |
| | Brood Size | 1.36 ± 0.31 | 1,88 | 19.30 | **<0.001** |
| | Body Condition | -24.07 ± 7.83 | 1,74 | 9.45 | **0.003** |
| | Feather Hue | 0.005 ± 0.019 | 1,64 | 0.06 | 0.81 |
| | Year | -0.64 ± 0.63 (2017) | 1,99 | 1.01 | 0.32 |
| | Body Condition*Hue | 0.05 ± 0.02 | 1,74 | 9.30 | **0.003** |
| Female DR | | | | | |
| | Habitat Type | -4.64 ± 2.25 (grass) | 1,63 | 4.26 | **0.043** |
| | Brood Size | 0.36 ± 0.33 | 1,73 | 18.60 | **<0.001** |
| | Nestling Stage | 1.71 ± 0.48 (middle)<br>3.01 ± 0.67 (late) | 2,119 | 12.03 | **<0.001** |
| | Year | 0.51 ± 0.46 (2017) | 1,134 | 1.25 | 0.27 |
| | Habitat * Brood Size | 1.26 ± 0.45 (grass) | 1,69 | 7.71 | **0.007** |

[1] Each variable's coefficient estimates (unstandardized) were obtained using the "summary" function in R and the degrees of freedom, F, and *P*-values were obtained using the "anova" function. For categorical variables, the coefficient is calculated for the category in parentheses to compare to the intercept (the category of the variable not indicated in parentheses), but the other columns refer to the categorical variable as a whole.

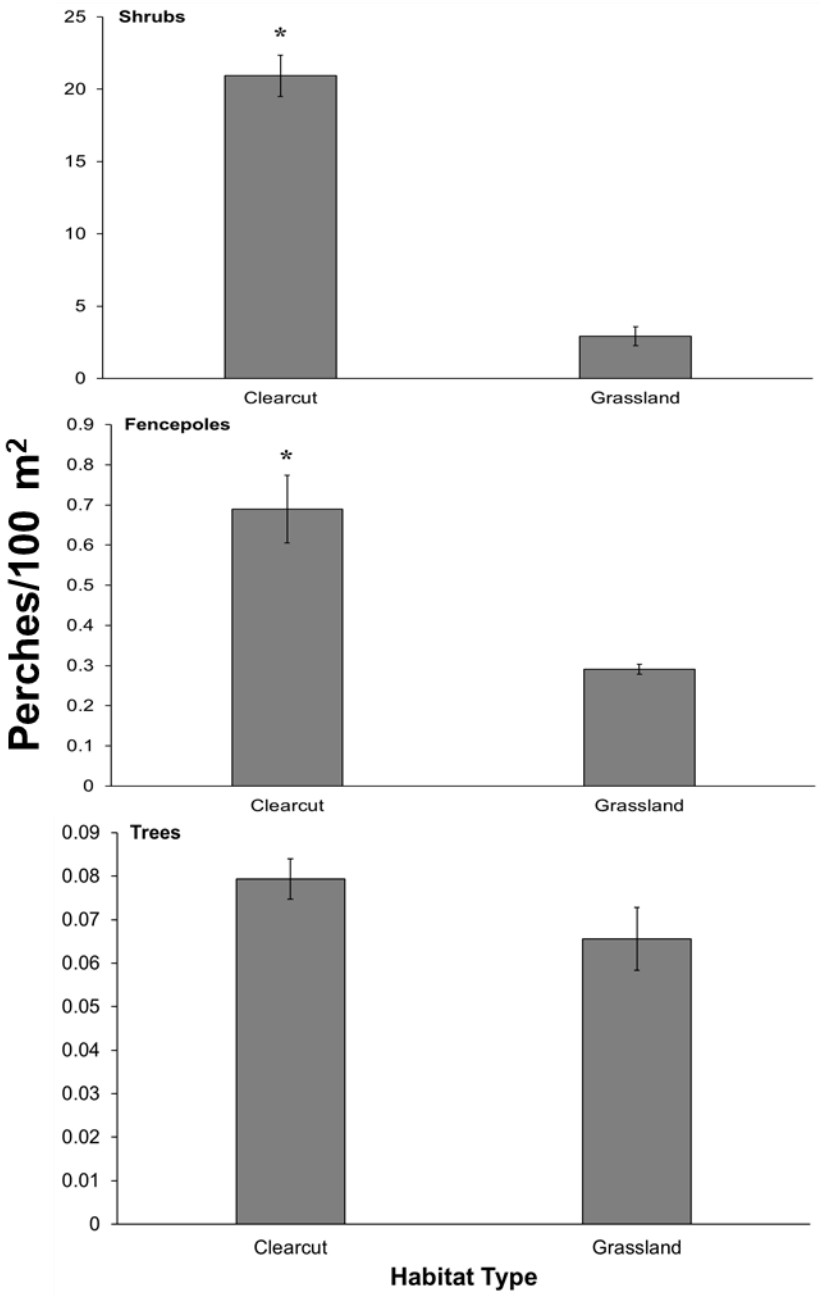


**Figure 2.1.** The average number of perches/100 $m^2$ (+/-SE) in each habitat in central British Columbia that could be used by mountain bluebirds. Shrub-sized perches are 0.5-1.5 metres tall, fencepole perches are 1.5-3 metres tall, and tree perches are over 3 metres tall. The stars indicate a significant difference ($P < 0.05$), as shown by t-tests, between the habitats. I sampled perches for 44 clearcut nestboxes and 52 grassland nestboxes.

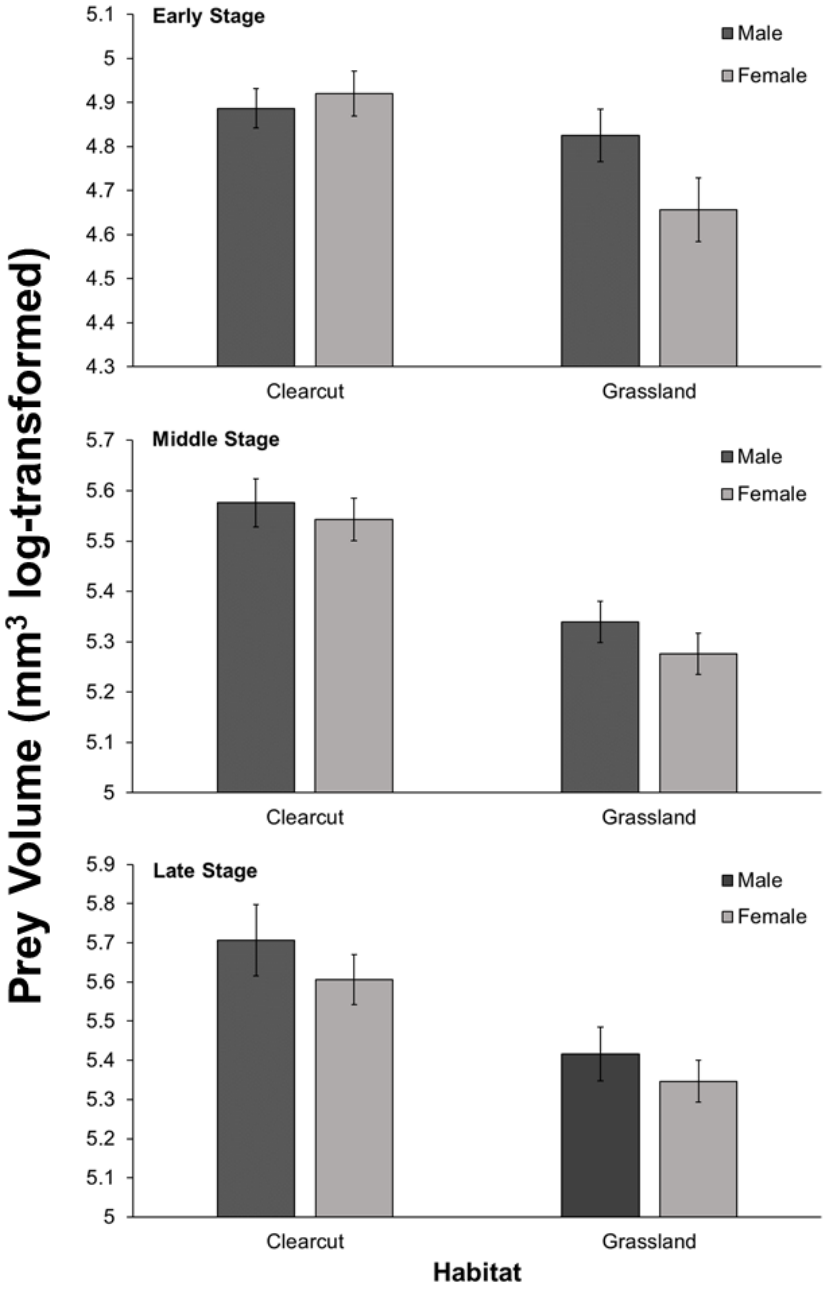


**Figure 2.2.** Prey volume brought by mountain bluebird males and females in clearcuts and grasslands in central British Columbia separated by nestling stage (early: 0-4 d old; middle: 5-11 d old; late: $\geq$ 12 d old). Bars are means +/- standard error. In the early nestling stage, there were 37 clearcut boxes and 26 grassland boxes. The middle nestling stage had 40 clearcut boxes and 35 grassland boxes. The late nestling stage had 12 clearcut boxes and 16 grassland boxes.

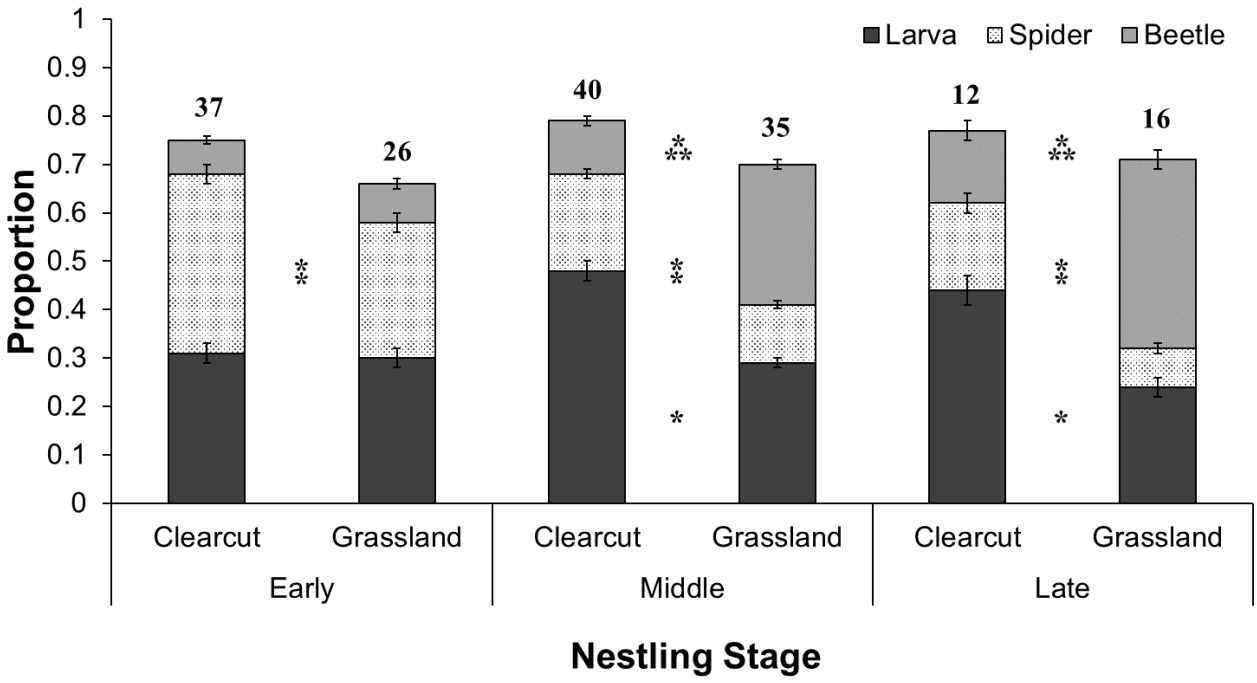


**Figure 2.3.** The average proportion of prey that were larvae, spiders, or beetles brought at different nestling stages (early: 0-4 d old; middle: 5-11 d old; late: ≥ 12 d old) in central British Columbia. These were the three most dominant prey classes brought by mountain bluebird adults. The error bars are standard error. The stars indicate if the habitats were significantly different within a stage ($P < 0.05$; larva: *, spider: ⁂, beetle: ⁂). The number of boxes with filming data are above the columns.

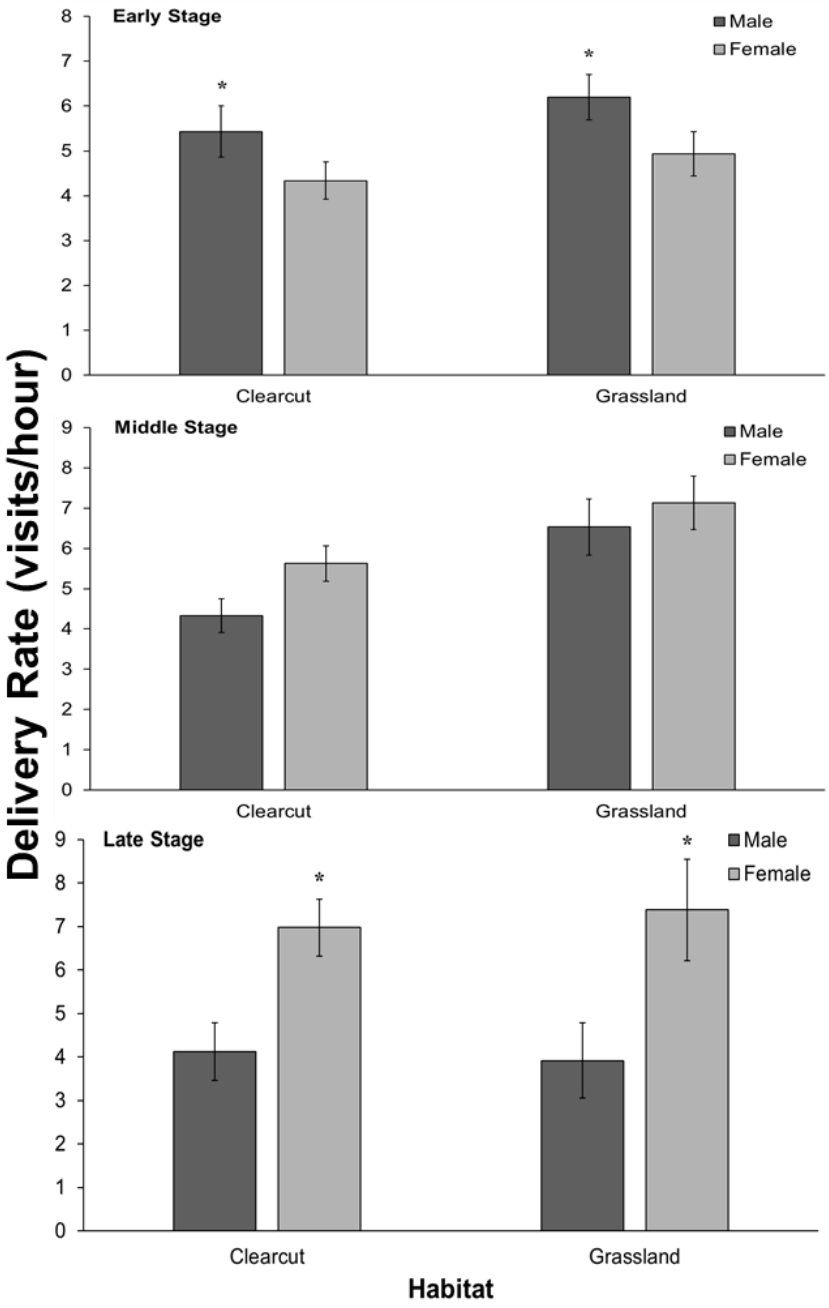


**Figure 2.4.** The average delivery rates by sex in clearcuts and grasslands broken up by nestling stage for mountain bluebirds (early: 0-4 d old; middle: 5-11 d old; late: ≥ 12 d old) in central British Columbia. The stars indicate a significant difference between the two sexes ($P < 0.05$). In the early nestling stage, there were 37 clearcut boxes and 26 grassland boxes. The middle nestling stage had 40 clearcut boxes and 35 grassland boxes. The late nestling stage had 12 clearcut boxes and 16 grassland boxes.

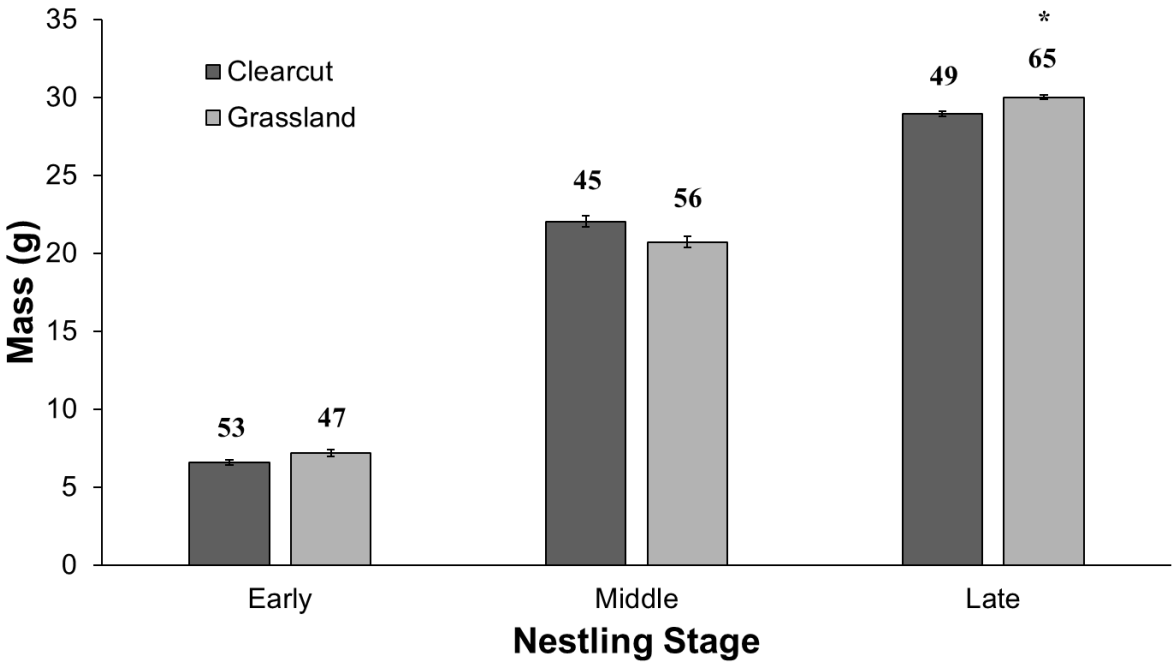


**Figure 2.5.** The mean mass of mountain bluebird nestlings at each nestling stage (early: 0-4 d old; middle: 5-11 d old; late: ≥ 12 d old) in both habitat types in central British Columbia. Sexes were pooled in the figure for illustration. The star indicates a significant difference ($P < 0.05$) between habitats in the late nestling stage (fledglings). The number of nests in which nestlings were weighed are above the columns.

# CHAPTER 3: REPRODUCTIVE SUCCESS AND PHYSICAL ATTRIBUTES OF BLUEBIRDS IN GRASSLAND AND CLEARCUT HABITATS

## 3.1 Introduction

In normal circumstances, animals have evolved to recognize cues of habitat quality and according to the classic despotic model of settlement (Fretwell and Lucas 1969), the higher-quality, more competitive territorial birds should first settle in the best quality habitat (Hildén 1965). When these habitats become saturated, lower-quality birds or those that arrive in the breeding grounds later are forced into suboptimal habitats. However, ecological traps may arise if individuals do not recognize that an anthropogenically altered habitat is inferior to their natural habitat and so settle there, resulting in poor reproductive fitness even for higher-quality individuals in the population (Schlaepfer et al. 2002; Kristan 2003; Battin 2004). As the proportion of habitat that is an ecological trap increases on the landscape, it could result in a decrease in the overall population size (Delibes et al. 2001; Donovan and Thompson 2001).

In temperate forests of North America, some researchers have proposed that clearcuts created by forestry are ecological traps for breeding birds, mostly because of high predation rates in such habitats (Robertson and Hutto 2007; Tozer et al. 2012). However, there is little information on the relative quality of individuals that settle in clearcuts, and on how clearcut habitat might affect reproductive success by mechanisms other than nest predation. Mountain bluebirds (*Sialia currucoides*) are a thrush of open grassland habitats but readily settle in clearcuts (Holt and Martin 1997). A previous study on mountain bluebirds proposed that clearcuts were ecological traps because of high predation rates (Holt and Martin 1997), but it is unknown how generalizable nest predation rates are, or whether other factors such as food supply in clearcuts could also influence reproductive outcomes.

Prey quality and abundance can affect reproductive parameters such as laying date, clutch size, incubation period, and egg size. Experiments have shown that supplemental food provided to a variety of bird species in the wild may lead to earlier laying dates (Reynolds et al. 2003; Harrison et al. 2010), larger clutches (review in Christians 2002), or larger eggs (Wiebe and Bortolotti 1995). In turn, larger eggs can positively affect hatching success, nestling growth, and

fledging success (Amundsen et al. 1996; Budden and Beissinger 2005; Whittingham et al. 2007). A greater availability of prey can also result in shorter incubation periods (Harrison et al. 2010) because the female needs fewer and shorter recesses to forage (Amininasab et al. 2016), maintaining greater incubation constancy and accelerating embryonic development. Finally, numerous experiments also show that food supplementation allows nestlings to grow faster (Garcia et al. 1993), reach higher fledgling masses (Bańbura et al. 2011; Perrig et al. 2014), and/or to attain a bright or ornamented plumage that may signal quality (Doyle and Siefferman 2014). Overall, more food may have a positive effect on many reproductive parameters, so a difference in the abundance or quality of prey between clearcuts and grasslands might be manifested at several stages of breeding.

If clearcuts are ecological traps, mountain bluebirds that settle there will be of higher or similar quality compared to grasslands. Quality can refer to adult age (as older adults are more experienced), body size and condition, or cues of health or nutritional status such as feather colour. Brightly-coloured plumage may signal age, health, or foraging ability (Linville et al. 1998; Hill 2006; Pagani-Núñez and Senar 2014). Morrison et al. (2014) found that female mountain bluebirds with more UV-blue tails had larger clutches and Siefferman and Hill (2003; 2005) found that eastern bluebirds (*Sialia sialis*) with brighter and more UV-shifted blue colouration invested more in their offspring, resulting in nestlings in higher condition. Blue colour in feathers is produced by precise alignment of microstructures in the barbules, and the intensity of structural colouration can be reduced even with minor nutritional stress as the feather grows (Hill 2006), so it is a good indicator of nestling quality as well. The blue colour in eastern bluebird feathers depends at least partially on condition and not only genes (Doyle and Siefferman 2014). Therefore, feather colour is a good indicator of quality in both adult and nestling mountain bluebirds.

If clearcuts are ecological traps because of lower food availability, I predicted that adults that settled there would be of similar age and quality (or higher quality) compared to adults in grasslands. If adults are of equivalent quality when they settle in the two habitats, I also predicted that nest building should occur around the same time in both habitats (indicating arrival on the breeding grounds), but that reproductive output (e.g. laying date, clutch size, or egg volume) would be delayed or lower in clearcuts than in grasslands. If females are energetically stressed due to lack of food in clearcuts, I predicted that they would spend less time incubating each day

as they forage for themselves, resulting in a longer incubation period and lower hatching success. Fledging success and nestling quality, as measured by fledging mass, feather colour, and immune response, would also be lower in clearcut habitats.

Alternatively, if clearcuts are not ecological traps but instead are perceived as secondary habitats by the birds, adults settling in clearcuts should be the least competitive in the population (i.e. younger and/or of lower quality compared to the adults in grasslands), and nest building should start later in clearcuts. A third alternative is that clearcuts and grasslands are equally suitable for mountain bluebirds, in which case adult quality and reproductive parameters should not differ between the two habitats. Finally, if clearcuts are better-quality habitats than grasslands, adults that settle in the former habitat should be of similar or better quality and have better reproductive success compared to grasslands.

I also predicted that nestling survival and quality would be positively correlated with measures of parental quality in each habitat, but perhaps more so in clearcuts. If clearcuts are lacking food, then older, better-quality adults might be able to cope with higher foraging demands better than lower-quality, yearling adults such that differences between individuals of different age or quality would be accentuated in a more stressful habitat.

## 3.2 Methods

### *3.2.1. Study Site and Study Species*

I studied mountain bluebirds at three study locations in central British Columbia during the breeding seasons of 2016 and 2017. Various grassland sites were located near Riske Creek (51°58’ N, 122° 31’ W, 986 m a.s.l.), 100 Mile House (51° 38' N, 121° 17' W, 970 m a.s.l.), and Bridge Lake (51° 28' N, 120° 43' W, 1140 m a.s.l.), with clearcut sites near the latter. Over 300 plywood nestboxes were placed on fenceposts in grazed grasslands, which contained native and introduced grasses and forbs, and on retained trees in 14 logging cuts that were between 10-45 ha in size and 1-6 years post-harvest. All boxes were at least 400 m apart. The clearcuts were originally mixed forests that included Douglas fir (*Pseudotsuga menziesii*), trembling aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), and white and hybrid spruce (*Picea glauca* and *P. glauca* X *engelmannii*). The sites were close enough to each other to experience similar weather patterns, and preliminary analyses showed no significant (general linear model: $P$=0.09) site differences in ambient daily temperatures in May and June, as monitored by iButtons at nestboxes. Similarly, preliminary models of reproductive parameters did not show

"site" to be a significant factor, so to simplify models it was deleted from subsequent analyses. In clearcuts, several boxes were fitted with a sheet of metal flashing at the base of the trunk beneath the box to deter predators, but predation rate did not differ between nests with and without metal ($\chi^2_1$<0.001, $P$=1), so all such boxes were included in analyses of nest success.

Mountain bluebirds begin to settle on the sites around mid-April (after migration) and lay clutches of 5-6 eggs on average (Power and Lombardo 1996). Only the female builds the grass nest inside the box and incubates, but both sexes provision the offspring with a variety of invertebrate prey, including Lepidoptera (adults and larvae), Arachnida, Coleoptera, Orthoptera, and Hymenoptera (Power 1980; Herlugson 1982).

*3.2.2 Field Work*

Nestboxes were checked regularly every 3-4 days from about 24 April to record the presence and amount of grass inside, as well as the timing of laying, clutch sizes, hatching success, and fledging success. I monitored 84 pairs in 2016 and 59 pairs in 2017. After clutch completion, the length and width of eggs were measured with digital calipers, and egg size (volume) was calculated according to the equation: 0.504*length*breadth$^2$, where 0.504 was a standard for thrush eggs (Hoyt 1979). When clutches were complete and females had been incubating for at least six days, I placed iButton temperature loggers (Maxim Integrated, San Jose) in 25 clearcut and 26 grassland nests in 2016, and 14 clearcut and 15 grassland nests in 2017, to record incubation behaviour. The iButtons were attached to a wire, which was threaded through the nest material and fastened to the floor of the box to deter females from moving them (similar to Johnson et al. 2013b). These iButtons took readings every 3 min for 2-3 days. I also put control iButtons underneath the nestbox to record ambient temperature. Recesses were defined as a period when the temperature dropped suddenly by at least 1.5° C (Walters et al. 2016) and ended when the temperature increased quickly back to the stable threshold temperature that indicated incubation at the box (this temperature varied slightly depending on the ambient temperature in the environment and position of the datalogger in the nest cup). The accuracy of the method was confirmed by direct observations of 5 incubating females. In all cases, drops in temperature readings reported by the iButtons closely aligned with the timing of observed absences from the nest.

Attempts were made to trap and band all adults at monitored boxes: 123 adults were caught in 2016 and 94 in 2017, using swing-door traps during late incubation and early nestling-

rearing. Birds were weighed, aged as adults versus yearlings based on molt (Pyle 1997), and given a unique combination of colour and aluminum bands for identification. Six length measures of structural size were taken: head-bill, culmen, 9th primary, central rectrix, tarsus, and flattened wing chord. I entered these measurements in a principal component analysis (one for each sex) and I used the score on the first axis (PCA1) as a measure of overall body size (Rising and Somers 1989). A body condition index was then calculated as the residual of a regression of body mass against PCA1 (Labocha and Hayes 2012; Wiebe and Vitousek 2015). Finally, I took the secondary feather S2 from the left wing of adults, for analysis of colour in the lab.

As measures of nestling quality, I used mass taken near fledging (15-16 d old) of nestlings at 64 boxes in 2016 and 49 boxes in 2017, and colour of the tip of secondary feather S2 clipped from nestlings at the same age. I also measured one aspect of immune function, T-cell mediated immunity, in a subsample of nestlings 13 days old. I randomly sampled one of each sex in each nestbox, excluding the runt if present. First, I measured the thickness of the nestling's wing web and then I injected 0.05 mL of 1 mg phytohemagglutinin (PHA-P) /mL of phosphate-buffered saline solution into the wing web. I measured the change in wing web thickness as an index of the strength of the immune response 24 hours later (Smits et al. 1999). Greater T-cell mediated immune responses are often found in well-fed nestlings (i.e. fed enough protein; Lochmiller et al. 1993), and nestlings with stronger T-cell responses often have faster growth rates (Whittingham et al. 2007) and longer life spans (Saino et al. 2012). Immune responses were measured for 56 nestlings from 31 boxes in 2016 (clearcuts: 31; grasslands: 25) and 47 nestlings from 25 boxes in 2017 (clearcuts: 30; grasslands: 17).

I analyzed feather colour with an Ocean Optics Flame Miniature Spectrometer with a DH-mini UV-VIS deuterium halogen light source and a white reflectance standard. Integration time was set to 325 ms, the average scans to 2, and the boxcar to 10. For each feather, I took three readings on the leading edge of the vein at 2.5 cm from the tip of the feather. The R library "pavo" (Maia et al. 2013) was used to obtain the variables of brightness, chroma, and hue (Montgomerie 2006; Berzins and Dawson 2016). Brightness is the average amount of light reflected by the feather on the spectrum within 300-700 nm (% reflected). There were two chroma variables, one for the UV range (300-400 nm) and one for the visible spectrum in the blue range (400-512 nm), which indicated the relative proportion of light reflected by the feather in their respective ranges relative to the entire spectrum. Lastly, hue was computed as the

wavelength of the maximum reflectance of the feather. Chroma varied little between individuals, so I chose to use the two uncorrelated variables of brightness and hue in subsequent analyses.

*3.2.3 Statistical Analyses*

To examine differences in characteristics of adults and in reproductive performance between clearcut and grassland habitats, we used mainly general linear models (LM, R version 3.4.3; R Core Team 2017), linear mixed effects models when an independent random factor was included (LMM, R library "lmerTest"; Kuznetsova et al. 2017) or generalized linear models when the dependent variable was binary or categorical (GLM). The R library "car" with the function "Anova" (Fox and Weisberg 2011) was used to obtain P values and chi-square values for GLMs. I report data as means $\pm$ standard error in the results section, unless indicated otherwise. Initial models included two-way interactions, but during model simplification, non-significant ($\alpha > 0.05$) interactions or variables were removed sequentially although habitat was retained in models as the main hypothesis of interest. The models' remaining explanatory variables are in Table 3.1, 3.2, 3.3, and 3.4. To examine whether parents were of better quality in one habitat, I used several models to analyze traits of parents separated by sex: 1) size (LM), using the explanatory variable of habitat type; 2) condition (LM) using habitat type, age, brood size, Julian date, and year as the explanatory variables; 3) age using a chi-square test; and 4) feather colour (two dependent variables of hue and brightness; LMs) with habitat type, age, size, condition, and year as explanatory variables. In the models for nest building, dates were binned into nine categories of 5-day length because nest visits were not frequent enough to determine the exact day that a female started adding grass to the box. Nest building GLMs (quasipoisson) originally included habitat type, all the female characteristics (age (adult versus yearling), size, body condition, feather brightness, and feather hue), and year as variables. Feather hue was log-transformed in every model that it was included as an explanatory variable.

For laying date, the LM included habitat type, all female characteristics, and year as explanatory variables. For the dependent variable of clutch size that was not normally distributed, I used two categories, $\leq$5 eggs and $\geq$6 eggs, in a generalized linear model with a binomial distribution, containing habitat type, laying date, and female characteristics as the explanatory variables. I used a LM to analyze egg volume, with habitat type, laying date, clutch size category, all female characteristics, and year as explanatory variables.

The number of days that a female incubated the eggs (incubation period) was analyzed using a GLM (quasipoisson) with habitat type, laying date (log-transformed), clutch size category, egg volume, all female characteristics, and year as explanatory variables. I ran LMMs for the dependent variables of number of recesses/hour, average recess length, and the total time that females were off the nest during the day (log-transformed). These models originally had habitat type, female age, female body condition, clutch size, average daily temperature outside of the nestbox, the day of incubation that the iButton was running, and year as fixed effects. The random effect was box number because there were 2-3 days of data for each box.

To analyze nesting success, I used chi-square tests to compare the frequency of nests between habitats that failed completely (due to predation or abandonment) versus ones that had at least one egg hatch or one nestling fledge. For hatching success, I excluded failed nests and used a GLM with a binomial distribution to analyze hatching proportion. This model had habitat type, laying date, egg volume, all female characteristics, and year as explanatory variables. The model for fledging success (proportion of the brood that fledged) was the same as for hatching success. We also used a chi-square test to compare the number of eggs that ended up fledging vs. the number of eggs that did not fledge between habitats. Finally, I used a GLM (quasipoisson) to determine if there was a higher count of fledglings overall in a certain habitat using habitat, laying date, egg volume, all female characteristics, and year as explanatory variables.

LMMs with nestbox as a random effect were used for dependent measures of nestling quality: fledgling mass, fledgling wing length, and T-cell immune response. LMs for feather hue and brightness (separated by sex) were used because we took a feather from only one nestling of each sex in each nestbox. All initial models included year, nestling sex, age of female parent, date, and habitat type as explanatory variables. The models for wing length and colour also included nestling age because feathers were still growing at the time they were measured. Models of feather colour also included brood size in the initial model and the model for immune responses also included fledgling mass.

## 3.3 Results

### *3.3.1 Adult Quality and Settlement of Habitat Types*

Habitat type was not associated with female size, feather hue, or feather brightness, but females in clearcuts had lower body condition (-0.51 $\pm$ 0.27) than those in grasslands (0.17 $\pm$ 0.20; Table 3.1). Female age did not differ between habitats (36% yearlings in clearcuts and 34%

yearlings in grasslands; $\chi^2_1$<0.001, *P*=1). However, there were age effects with older females being in higher body condition and having bluer feathers than yearlings, but age did not affect female feather brightness (Table 3.1). For male traits, there was no association between habitat type and body condition, feather hue, or brightness, but males in clearcuts were larger (PCA1 score: 0.35 $\pm$ 0.17) than males in grasslands (-0.10 $\pm$ 0.12). The age of males did not differ between habitats (35% yearlings in clearcuts and 47% yearlings in grasslands; $\chi^2_1$=1.10, *P*=0.29). Older males had higher body conditions, bluer feather hues, and brighter colours (Table 3.1). Since there was no interaction between adult age and habitat, any differences between individuals attributable to age would have been similar across the habitat types.

Adults in clearcuts initiated nest building earlier (26-30 April) than those in grasslands (1-5 May; Table 3.2). Nest initiation was also earlier for bluebirds older than one year compared to yearlings (Figure 3.1), but the difference was within a span of five days. Nest initiation was also earlier for females with a less blue feather hue. When nest building began, birds took the same amount of time to build nests in both habitats (approximately 5 days).

*3.3.2 Egg Laying*

Females with brighter feathers laid eggs earlier, and there was an interaction between age and habitat (Table 3.2). In grasslands, yearlings laid their first egg later than older birds while laying dates did not differ with age in clearcuts (Figure 3.1). Females in clearcuts had larger clutches than those in grasslands (Table 3.2). About 58.6% of nests in clearcuts (n = 61) had six or more eggs while only 40.5% of nests in grasslands (n = 82) did so. Analysis of the laying date * female age interaction showed no change in clutch size with date for yearlings, but older females were more likely to have 5 or less eggs later in the breeding season. Egg volume did not differ between habitat types, but it increased with laying date. No female characteristics affected egg volume.

*3.3.3 Incubation Behaviour*

Incubation periods were similar between habitats (Table 3.3) and were 14 $\pm$ 0.1 days. The interaction effect of feather hue and laying date showed that the incubation period of bluer females did not vary with date, whereas the incubation period of less blue females became shorter with date. The length of recesses did not vary with habitat, but the number of recesses per hour was related to an interaction between habitat and average daily temperature (Table 3.3; Figure 3.2). In grasslands, females took more recesses as ambient temperatures became warmer,

but in clearcuts there was no effect of temperature. Furthermore, the interaction between ambient temperature and incubation day showed that when ambient temperature was cold, very few recesses were taken when embryos were young, but more were taken later in the incubation period. However, when it was warm, there was no trend in the number of recesses with different ages of embryos.

No traits of females affected the number of recesses, but for recess length, there was an interaction between body condition and age (Table 3.3). Among birds in lower body condition, yearlings took longer recesses than older birds, but among birds in higher condition, older birds took slightly longer recesses than yearlings. (Figure 3.3). Also, birds of all ages shortened their incubation recesses as the temperature increased, but this pattern was more pronounced among yearlings than older birds (Figure 3.2). Finally, no variables were associated with the total time that females spent off their eggs each day.

*3.3.4 Nest Success*

Approximately 90% of all nests hatched at least one egg, and this index of nest success did not differ between habitats ($\chi^2_1$=0.12, *P*=0.73). Of those nests that hatched at least one egg, the proportion of eggs that hatched also did not differ between habitats (Table 3.2). However, older females in both habitats hatched a higher proportion of their eggs (0.93 $\pm$ 0.02) than yearlings (0.85 $\pm$ 0.03; Table 3.2). When causes of nest failure were determined, more nests were abandoned in clearcuts (22% of 77 nests) compared to grasslands (10% of 109 nests; $\chi^2_1$=4.18, *P*=0.041) and this was driven mainly by high abandonments in clearcuts in 2016. Predation rate (16%) did not differ between habitats ($\chi^2_1$= 0.001, *P*=1).

*3.3.5 Nestling Number and Quality*

Roughly 68% of 56 nests in clearcuts (first nesting attempts) fledged at least one nestling, while 83% of 70 nests in grasslands did so, but the trend to higher fledging success in grasslands was not significant ($\chi^2_1$=3.08, *P*=0.079). Of those nestboxes that fledged at least one individual, the proportion of the brood that fledged did not differ between habitats (90% fledged; Table 3.2). By the end of the breeding season, the average number of fledglings produced in nests that fledged at least one nestling was similar between the habitats (4.5 $\pm$ 0.1; Table 3.2). No female characteristics affected the proportion or number of nestlings that fledged. The overall productivity of first nests averaged over all eggs laid in each habitat was lower in clearcuts than

in grasslands: 54% of 325 eggs in clearcuts produced a fledgling whereas 63% of 404 eggs in grasslands did so ($\chi^2_1$=6.0 $P$=0.015).

Fledglings in grasslands weighed 3.7% more on average than fledglings in clearcuts (Table 3.4; Figure 3.4), but habitat did not affect other attributes such as wing length or brightness. Among female nestlings, those fledging in grasslands were bluer (lower hues) than females in clearcuts. The average female fledgling feather hue was 506.9 nm $\pm$ 1.8 in grasslands and 513.5 nm $\pm$ 2.0 in clearcuts. The female parent's age only affected wing length of the offspring (yearling: 64.4 $\pm$ 0.6 mm; adult: 65.3 $\pm$ 0.4 mm). Brood size did not affect any measure of feather colour in either sex. T-cell mediated immune responses did not vary according to habitat types or sex, but stronger immune responses (larger swelling of wing webs) were seen in heavier nestlings (Figure 3.5).

## 3.4 Discussion

Overall, the age and quality of adults settling to breed in clearcuts appeared similar to those in grasslands, which suggests that adults did not perceive the anthropogenically created habitats as low quality. General productivity in terms of fledglings produced per eggs laid was higher in grasslands and those fledglings appeared to be of better quality which suggests clearcuts were an ecological trap, although many parents managed to raise offspring there. Habitat effects were seen at a few stages of breeding as outlined in more detail below.

### *3.4.1 Adult Quality and Settlement of Habitat Types*

Male bluebirds but not females were larger in clearcuts than grasslands, but other traits signaling quality (colour and age) did not differ between habitat types for either sex. In some other passerine species, larger birds are better competitors for resources and territories (Gustafsson 1988; Pérez-Tris and Telleria 2002), and perhaps intraspecific competition for clearcut sites was more intense, but the significance of body size in bluebirds for securing preferred sites, if any, is unknown. Hollander et al. (2012) reported that red-backed shrikes (*Lanius collurio*) in the preferred low-quality habitat (ecological trap) were more aggressive than those in the native habitat, indicating that the birds settling in the ecological trap habitat were the more competitive, higher-quality birds (Hollander et al. 2011). Generally, the quality of settling breeders did not differ substantially between the habitats in my study, which is a necessary condition for an ecological trap. Therefore, clearcuts do not seem to be a "severe trap," but rather

an “equal-preference trap” (Robertson and Hutto 2006), because clearcuts did not attract the highest quality individuals in the population.

Body condition of parents was measured in the early to mid-nestling stages, by which time prey abundance and foraging effort probably affected mass. The body condition of males, which probably did not put as much effort into their broods as females at early stages, did not vary with habitat. Garcia et al. (1993) found that male mountain bluebirds did not have significantly different body masses regardless of if they were supplemented with food. Females, on the other hand, had poorer body condition in clearcuts compared to grasslands in my study, and lower mass when not supplemented with food in the study by Garcia et al. (1993). This might be a result of a lower prey abundance in clearcuts, since delivery rates of females were lower in clearcuts compared to grasslands and females were unable to increase their delivery rate in clearcuts with increasing brood size (Chapter 2). Therefore, clearcuts were an ecological trap, but mainly females were negatively affected by the energetic stress of rearing offspring there. However, I did not catch the adults repeatedly during the season so trajectories of mass gain or loss in the habitats are unknown.

Earlier arrival and settlement after migration in one habitat type versus the other is a clue to whether individuals prefer the lower-quality habitat (review in Robertson and Hutto 2006). The initiation of nest building was earlier in clearcuts, indicating that bluebirds perhaps perceived clearcuts as quality habitats and preferred to settle there first. Hollander et al. (2011) and Söderström and Karlsson (2011) found that red-backed shrikes also arrived in clearcuts before grasslands (farmlands) in Europe and appeared to prefer clearcuts, so the openness and physical structure of these anthropogenically created habitats seems to be attractive for some grassland birds. Preference assumes that individuals have a chance to sample a range of habitats and actively choose but I could not determine whether individual bluebirds in my study sampled both habitat types before settling. Another option is that they just encountered a clearcut before a grassland and decided to settle there based on the cues available. In that case, there may be no active selection or preference of the different habitats and individuals of both high and low quality may settle in the habitat type they happen to encounter first.

Regardless of habitat, older mountain bluebirds started constructing their nests earlier than yearlings, which is a common pattern in other birds because yearlings often arrive later (Cooper et al. 2009; Cadahia et al. 2017). The finding that less-blue females started depositing

nest material sooner is hard to explain, but perhaps poorer quality females tried to retain a nest site by signalling box occupancy at an early stage. Since hue did not affect laying date, both high- and low-quality females started laying eggs around the same time, which means there would have been a longer period between nest building and laying in these less-blue females.

*3.4.2 Egg Laying*

Early laying dates in the breeding season are usually beneficial because there is more time for a second nest attempt if the first fails, or for a second brood once the first one fledges (Kelly and Van Horne 1997; Wilson and Arcese 2003). Consistent with the pattern found in many other passerine species, older females in the population begin laying earlier (Balbontín et al. 2012; Germain et al. 2015), but in my study, this pattern was seen only in grasslands and not clearcuts. The relatively delayed nesting of yearlings in grasslands (Figure 3.1) may be a result of more intense competition for nestboxes in grassland sites. The abundance of a box competitor, the tree swallow (*Tachycineta bicolor*; Munro and Rounds 1985; Wiebe 2016), was higher in grassland sites, so inexperienced yearlings may have found it especially difficult to quickly initiate laying there. Generally, females were not more delayed in clearcuts, suggesting food was sufficient there in early spring to develop and maintain adequate energy to initiate egg laying. Females that were of better quality, as indicated by brighter feathers, also initiated relatively early, similar to some other studies which have found that females with greater plumage ornamentation are able to lay eggs earlier (Parejo et al. 2011; Wiebe and Vitousek 2015).

Another indication that prey abundance or quality in clearcuts in early spring was relatively high was that females there had slightly larger clutch sizes than females in grasslands. Nestling diets in clearcuts indicated a high fraction of nutritious prey there (see Chapter 2) and this could indicate that females in clearcuts had access to energy-rich items which facilitated egg formation. Cooper's hawks (*Accipiter cooperii*) also had larger clutches in an ecological trap habitat compared to the higher quality, less preferred habitat (Boal and Mannan 1999). As is typical for many other bird species, clutch size also declined with laying date (Ramsay and Houston 1997; Koch et al. 2012; Adamou et al. 2015), although this occurred only in adults and not yearlings. Perhaps the greater experience of older birds allowed them to invest more heavily in egg production at the earliest breeding dates.

Larger eggs can result in better hatching success, nestling growth, and fledging success (Amundsen et al. 1996; Budden and Beissinger 2005; Whittingham et al. 2007), but egg volume

of bluebirds showed little variation related either to habitat type or to female traits. Egg volumes increased slightly with date but there was no clear relationship with clutch size, so any trade-off between number of eggs and egg size as found in some other species (Cichon 1997; Styrsky et al. 1999; Song et al. 2016) did not seem to be strong in mountain bluebirds. Apparently, females invested more energy in eggs later in the season either as food supply became more abundant or as other energy costs, such as thermoregulation, declined. Other birds such as eastern phoebes (*Sayornis phoebe*) probably increased their egg mass as the season progressed because food became more abundant later in the season (Murphy 1994).

*3.4.3 Incubation Behaviour and Hatching Success*

During incubation, a female faces energetic trade-offs between warming the eggs versus leaving the clutch to forage for herself (Wiebe and Martin 1997). Decisions about how much recess time to take may be complex because costs and benefits are mediated by several factors, including ambient temperature (Klimczuk et al. 2015; Walters et al. 2016), the female's own body condition (Bueno-Enciso et al. 2017), and perhaps predation risk to the female or clutch (Massaro et al. 2008). For mountain bluebirds, the effect of habitat was only apparent in an interaction with ambient temperature and was related to the number of recesses. Females in grasslands but not clearcuts took more recesses as the ambient temperatures increased, but females in grasslands took fewer recesses than females in clearcuts at low temperatures. A more detailed study about the dynamics of female condition is needed to determine the cause, but my results suggest that females may have been in higher condition in grasslands during incubation. Therefore, the females in grasslands were better able to maintain incubation constancy during stressful (cold) ambient temperatures and perhaps recouped energy reserves by foraging in warmer temperatures when eggs were less likely to chill. I also found that, at least at low temperatures, the number of recesses increased with incubation day, similar to a pattern in barnacle geese (*Branta leucopsis*; Tombre et al. 2012). Developing embryos begin to generate some metabolic heat at later stages of incubation (Drent 1970), and so may be more able to buffer short absences of the female from the nest.

When body condition was low, yearlings took longer recesses than older birds as though young birds were more willing to sacrifice incubation effort to forage for themselves. A similar age-related pattern of investment was shown experimentally in female tree swallows that had flight feathers clipped to make them lower quality; yearlings were also more willing to sacrifice

incubation effort than older swallows (Ardia and Clotfelter 2007). However, it is counterintuitive that female bluebirds (especially yearlings) took longer recesses during cold weather (Figure 3.2). Blue tit (*Cyanistes caeruleus*) females take shorter recesses in colder ambient temperatures but also take shorter recesses when there is more food available around their nest (Amininasab et al. 2016). Insects are quite likely less active and visible in cold temperatures, so perhaps it took females longer to find prey and satiate themselves during colder temperatures, requiring longer recesses. When considering total time off the nest during a 24 h period, incubation constancy for bluebirds did not differ between habitat types. Similarly, Amininasab et al. (2016) found that nest attentiveness by female blue tits did not differ between high- and low-quality habitats overall, although they did take shorter recesses in high-quality habitats. In fact, overall nest attentiveness in bluebirds was unrelated to any characteristic of the female or environment I measured, although in studies of other birds, attentiveness has decreased with poorer body condition (Wiebe and Martin 1997), with warmer temperatures (Zhang et al. 2017), and with lower food abundances (Rauter and Reyer 1997).

Incubation period did not vary between habitats, but for early-nesting mountain bluebirds, the incubation period was longer for less-blue females. This suggests that females of lower quality (as indicated by plumage colour) may be poorer foragers, as has been shown in northern cardinals (*Cardinalis cardinalis*) and eastern bluebirds (Linville et al. 1998; Siefferman and Hill 2005). Therefore, these lower quality females probably had inconsistent incubation behaviours, leading to longer development times for eggs. In my study, incubation periods decreased in dull females as the season progressed, probably as food became more available, although female colour does not affect female mountain bluebird provisioning in studies by Balenger et al. (2007) and Morrison et al. (2014). Black brants (*Branta bernicla nigricans*) nesting early in the season also had long incubation periods, but these decreased with laying date, perhaps to avoid high predation risks (Eichholz and Sedinger 1998). Generally, incubation constancy and incubation periods did not vary between habitats in mountain bluebirds, which may explain why hatching success was also similar between habitats. Older females were able to hatch a larger fraction of their eggs than younger females, suggesting they were more experienced at regulating egg temperatures and laying fertile eggs as has been shown in some other species (Blem et al. 1999; Wilcoxen et al. 2011).

Other studies have reported that some ecological traps may not have negative effects on a population until after hatching (Boal and Mannan 1999; Lloyd and Martin 2005; Robertson and Hutto 2007). Since laying date, clutch size, egg size, incubation behaviour, and hatching success were similar or better (clutch size) in clearcuts compared to grasslands in my study, the negative effects of this ecological trap may not have been present until later in the breeding period.

*3.4.4 Nest Success*

More nests were abandoned, especially in 2016, in clearcuts than in grasslands. There was a severe cold weather event with snow and sleet in late May at the time of most abandonments that year. The lower body condition of females in clearcuts could explain the increased abandonment in clearcuts compared to grasslands, as these individuals would have been less able to handle the extra stress of cold conditions in addition to the food stress. However, nest loss due to predation was similar between habitats, which is contrary to studies which have found that predation is high in clearcuts compared to a variety of open or treed habitats (De Santo and Willson 2001; Robertson and Hutto 2007; Tozer et al. 2012). The main predators in clearcuts at our sites were sciurids (red squirrel *Tamiasciurus hudsonicus*; northern flying squirrel *Glaucomys sabrinus*; least chipmunk *Tamias minimus*) and black bears (*Ursus americanus*), and the main predators in grassland sites were deer mice (*Peromyscus maniculatus*) and black bears. Another study of mountain bluebirds using nestboxes in clearcuts in southeastern British Columbia (Holt and Martin 1997) found predation rates of 50%, which was greater than the 16% in clearcuts on my sites. In both studies, bluebirds used boxes which were located in the middle of a clearcut (away from forest edges) so the much higher predation in the former study may be due to a higher density of predators there.

Holt (1997) reported a 52% predation rate for mountain bluebirds in natural cavities and a 47% predation rate in nestboxes in clearcuts, suggesting that predation risk was similar between artificial and natural nest cavities. However, Robles and Martin (2013) monitored natural cavities of bluebirds on one of my grassland sites and reported that only 56% of those fledged at least one nestling compared to the higher success in my grassland nestboxes (83%). Predators were directly implicated in 57% of the cases of known nest failure in natural cavities (Robles and Martin 2013). Most of the natural cavities used by bluebirds were created by northern flickers (*Colaptes auratus*), and so had larger entrances than the nestboxes, which might make the

artificial nests more difficult for predators to access. The fitness cost of many ecological traps is driven by high predation there (review in Battin 2004) but this was not the case in my study.

*3.4.5 Nestling Number and Quality*

Among nests that fledged at least one young, the proportion of the brood that fledged did not differ between habitats. Despite a slightly larger clutch size in clearcuts, when the number of fledglings was averaged over all starting nest attempts, the overall number of fledglings/nestbox was the same in clearcuts as grasslands. However, taking into account the unsuccessful nests (all eggs laid), overall productivity was about 9% lower in clearcuts. Fledgling mass was higher in grasslands compared to clearcuts, probably because of higher provisioning rates in grasslands (Chapter 2). Fledgling mass increases long-term survival and recruitment in many species (Monrós et al. 2002; review in Ronget et al. 2018). Therefore, offspring in the grassland habitat may be more likely to survive the post-fledging period. Hollander et al. (2011) found that red-backed shrikes had better nest success, larger brood sizes, and nestlings in better condition in farmlands (similar to grasslands) compared to their preferred habitat of the early-successional stage (similar to clearcuts) in spruce plantations in Belgium (an example of an ecological trap). Conversely, Söderström and Karlsson (2011) reported more red-backed shrike fledglings were produced in clearcuts compared to grasslands in Sweden, although they did not report nestling body condition.

The only other difference in nestling quality between habitats was that female nestlings in grasslands were bluer than female nestlings in clearcuts. Siefferman and Hill (2007) found differences in the feather colour for eastern bluebird male, but not female, nestlings when comparing a stressed brood (experimentally enlarged brood) to a reduced brood with males from reduced broods being brighter. However, it would stand to reason if one habitat had more food available, that females would differ in colour as well. Nevertheless, male nestling colour did not differ between habitats. There may be a trade-off between mass and colour in male mountain bluebirds because brightness and mass were inversely correlated among male eastern bluebird nestlings if they were not supplemented with food, but males achieved both high mass and bright plumage when supplemented (Doyle and Siefferman 2014). If the grassland habitats in my study provided more food for nestlings than clearcuts (see chapter 2), male nestlings in grasslands might have been both heavier and bluer whereas those in clearcuts might have invested in plumage colour at the expense of body mass. Any nutritional differences between habitat types

did not translate into a significant difference in the overall ability of nestlings in those habitats to mount T-cell mediated immune responses although heavier nestlings could mount stronger immune responses than lighter nestlings, confirming a common pattern in other species (Merino et al. 1999; Soler et al. 1999; Musgrove et al. 2017).

In sum, the quality of adults settling in the two habitat types appeared to be the same, or better in clearcuts, consistent with the idea of an ecological trap and not the ideal despotic model, as high-quality adults do not recognize and avoid clearcuts as an inferior habitat. Although parents produced a similar number of offspring/nestbox in each habitat, those offspring were of inferior quality in clearcuts. Also, the larger clutch sizes found in clearcuts were offset by fewer eggs reaching fledging in clearcuts. Furthermore, female parents in clearcuts seemed to deplete their body condition to a greater extent than females in grasslands, which could put them more at risk of abandoning clutches or broods if weather conditions become stressful. Therefore, clearcut sites in my study are passive ecological traps with subtle fitness costs that were not manifested as immediate mortality of adults or offspring, but which may have longer term impacts on survival linked to body condition and quality. The level of predation risk appears to vary greatly between studies, and nest success related to different configurations of clearcuts and predator communities may largely determine the severity of ecological trap effects for mountain bluebirds.

**Table 3.1.** General linear models for dependent variables indicating adult quality of mountain bluebirds in grassland versus clearcut habitats in central British Columbia. Coefficients are shown with SE. Significant *P*-values from the models are bolded.

| Dependent Variable | Model | Females | | | | Males | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Coefficient[1] | DF | *F* | *P* | Coefficient[1] | DF | *F* | *P* |
| Size | | | | | | | | | |
| | Habitat | -0.03 ± 0.20 (grass) | 1,108 | <0.1 | 0.89 | -0.45 ± 0.20 (grass) | 1,97 | 5.2 | **0.03** |
| Condition | | | | | | | | | |
| | Habitat | 0.44 ± 0.31 (grass) | 1,108 | 5.3 | **0.024** | -0.08 ± 0.22 (grass) | 1,97 | <0.1 | 0.92 |
| | Age | -0.74 ± 0.33 (yearling) | 1,107 | 7.9 | **0.006** | -0.46 ± 0.22 (yearling) | 1,96 | 8.2 | **0.005** |
| | Date | -0.04 ± 0.01 | 1,106 | 11.1 | **0.001** | -0.03 ± 0.01 | 1,95 | 16.7 | **<0.001** |
| | Year | 0.59 ± 0.30 (2017) | 1,105 | 3.8 | 0.05 | 0.01 ± 0.22 (2017) | 1,94 | <0.1 | 0.96 |
| Feather Hue (nm) | | | | | | | | | |
| | Habitat | 1.18 ± 3.6 (grass) | 1,102 | 0.1 | 0.76 | -1.69 ± 2.6 (grass) | 1,93 | 0.1 | 0.74 |
| | Age | 22.32 ± 3.7 (yearling) | 1,101 | 36.00 | **<0.001** | 22.85 ± 2.6 (yearling) | 1,92 | 80.0 | **<0.001** |
| | Year | -2.89 ± 3.6 (2017) | 1,100 | 0.6 | 0.43 | -0.96 ± 2.6 (2017) | 1,91 | 0.1 | 0.72 |
| Feather Brightness | | | | | | | | | |
| | Habitat | -0.29 ± 0.30 (grass) | 1,101 | 0.8 | 0.38 | 0.38 ± 0.25 (grass) | 1,93 | 0.1 | 0.82 |
| | Age | -0.29 ± 0.31 (yearling) | 1,100 | 0.7 | 0.40 | -1.68 ± 0.25 (yearling) | 1,92 | 55.8 | **<0.001** |
| | Year | -0.22 ± 0.30 (2017) | 1,99 | 0.6 | 0.46 | 0.22 ± 0.25 (2017) | 1,90 | 0.7 | 0.39 |
| | Size | *NA* | *NA* | *NA* | *NA* | 0.25 ± 0.12 | 1,91 | 3.6 | 0.06 |

[1] Each variable's coefficient estimates (unstandardized) were obtained using the "summary" function in R and the degrees of freedom, F, and *P*-values were obtained using the "anova" function. For categorical variables, the coefficient is calculated for the category in parentheses to compare to the intercept (the category of the variable not indicated in parentheses).

**Table 3.2.** Models for reproductive parameters of mountain bluebirds nesting in either grassland or clearcut habitats in British Columbia. Nest initiation is the time that nesting material first appeared in the box and nest building time is the time span from start of nest building to nest completion. Laying date and egg volume use general linear models (LM) with *F* statistics whereas the other reproductive variables use generalized linear models (GLM) with $\chi^2$ statistics. Significant *P*-values are in bold.

| Dependent Variable | Model | Coefficient[1] ± SE | DF | *F* or $\chi^2$ | *P* |
|---|---|---|---|---|---|
| Nest Initiation | | | | | |
| | Habitat Type | 0.35 ± 0.10 (grass) | 1,42 | 12.2 | **<0.001** |
| | Female Age | 0.28 ± 0.13 (yearling) | 1,41 | 4.6 | **0.03** |
| | Female Feather Hue | -3.55 ± 1.28 | 1,40 | 7.8 | **0.005** |
| | Year | 0.62 ± 0.11 (2017) | 1,39 | 32.6 | **<0.001** |
| Building Time | | | | | |
| | Habitat Type | -0.13 ± 0.11 (grass) | 1,58 | 1.5 | 0.22 |
| | Year | 0.10 ± 0.11 (2017) | 1,57 | 0.9 | 0.36 |
| Laying Date | | | | | |
| | Habitat Type | -2.70 ± 1.71 (grass) | 1,92 | 1.0 | 0.32 |
| | Female Age | -0.99 ± 2.30 (yearling) | 1,91 | 7.4 | **0.008** |
| | Female Feather Brightness | -1.04 ± 0.46 | 1,90 | 9.2 | **0.003** |
| | Year | 9.04 ± 1.39 (2017) | 1,89 | 47.8 | **<0.001** |
| | Habitat Type * Female Age | 7.91 ± 2.97 | 1,88 | 7.1 | **0.009** |
| Clutch Size | | | | | |
| | Habitat Type | -1.22 ± 0.46 (grass) | 1,108 | 7.5 | **0.006** |
| | Laying Date | -0.15± 0.04 | 1,107 | 7.8 | **0.005** |
| | Female Age | -22.62 ± 8.46 (yearling) | 1,106 | 1.1 | 0.30 |
| | Year | 0.84 ± 0.53 (2017) | 1,105 | 2.6 | 0.11 |
| | Laying Date * Female Age | 0.18 ± 0.06 (yearling) | 1,104 | 8.0 | **0.005** |

| Dependent Variable | Model | Coefficient[1] ± SE | DF | $F$ or $\chi^2$ | $P$ |
|---|---|---|---|---|---|
| Egg Volume | | | | | |
| | Habitat Type | -0.03 ± 0.04 (grass) | 1,123 | 0.4 | 0.55 |
| | Laying Date | 0.01 ± 0.003 | 1,122 | 9.4 | **0.003** |
| | Year | 0.01 ± 0.05 (2017) | 1,121 | 0.1 | 0.80 |
| Hatching Proportion | | | | | |
| | Habitat Type | -0.38 ± 0.30 (grass) | 1,104 | 1.67 | 0.20 |
| | Female Age | -0.89 ± 0.29 (yearling) | 1,103 | 8.80 | **0.003** |
| | Year | -0.03 ± 0.29 (2017) | 1,102 | 0.01 | 0.92 |
| Fledging Proportion | | | | | |
| | Habitat Type | 0.35 ± 0.31 (grass) | 1,94 | 1.31 | 0.25 |
| | Year | 0.60 ± 0.32 (2017) | 1,93 | 3.64 | 0.06 |
| Fledging Numbers | | | | | |
| | Habitat Type | -0.02 ± 0.06 (grass) | 1,95 | 0.09 | 0.77 |
| | Year | 0.05 ± 0.06 (2017) | 1,94 | 0.62 | 0.43 |

**1** Each variable's coefficient estimates (unstandardized) were obtained using the "summary" function in R. For categorical variables, the coefficient is calculated for the category in parentheses to compare to the intercept (the category of the variable not indicated in parentheses). The degrees of freedom, F or $\chi^2$, and *P*-values were obtained using the "anova" function for LMs and the "Anova" function for GLMs.

**Table 3.3.** Models for incubation behaviour of mountain bluebirds nesting in grassland versus clearcut habitats in central British Columbia. Incubation period is the number of days from end of laying to hatching, recess number and length refer to the periods the female was off the eggs, and total time off nest is time during a 24-hour period the female was off the eggs. Incubation period is the only generalized linear model with $\chi^2$ statistics. The other models are linear mixed models with *F*-values. Significant *P*-values from the models are bolded.

| Dependent Variable | Model | Coefficient[1] ± SE | DF | *F* or $\chi^2$ | *P* |
|---|---|---|---|---|---|
| Incubation Period (days) | | | | | |
| | Habitat Type | 0.006 ± 0.02 (grass) | 1,85 | 0.12 | 0.73 |
| | Female Feather Hue | 36.25 ± 16.94 | 1,84 | 0.69 | 0.41 |
| | Laying Date | 45.91 ± 21.55 | 1,83 | 7.34 | **0.007** |
| | Year | 0.02 ± 0.02 (2017) | 1,82 | 1.22 | 0.27 |
| | Female Hue * Laying Date | -7.47 ± 3.48 | 1,81 | 4.59 | **0.032** |
| Recesses/hour | | | | | |
| | Habitat Type | -0.84 ± 0.33 (grass) | 1,206 | 7.42 | **0.007** |
| | Average Daily Temperature (ADT) | 0.06 ± 0.03 | 1,184 | 10.53 | **0.001** |
| | Incubation Day | 0.20 ± 0.05 | 1,180 | 15.78 | < **0.001** |
| | Year | 0.15 ± 0.08 (2017) | 1,207 | 3.87 | 0.05 |
| | Habitat * ADT | 0.06 ± 0.02 (grass) | 1,191 | 10.47 | **0.001** |
| | ADT * Incubation Day | -0.01 ± 0.004 | 1,181 | 9.90 | **0.002** |
| Recess Length (min) | | | | | |
| | Habitat Type | -0.48 ± 0.65 (grass) | 1,54 | 0.53 | 0.47 |
| | Female Age | 5.71 ± 1.88 (yearling) | 1,151 | 9.23 | **0.003** |
| | Female Body Condition | 0.29 ± 0.17 | 1,60 | 1.61 | 0.21 |
| | ADT | -0.03 ± 0.06 | 1,147 | 11.65 | < **0.001** |
| | Year | -0.79 ± 0.48 (2017) | 1,145 | 2.70 | 0.10 |
| | Female Age * Body Condition | -1.44 ± 0.66 (yearling) | 1,58 | 4.75 | **0.033** |
| | Female Age * ADT | -0.43 ± 0.14 (yearling) | 1,150 | 9.51 | **0.002** |

| Dependent Variable | Model | Coefficient[1] ± SE | DF | $F$ or $\chi^2$ | $P$ |
|---|---|---|---|---|---|
| Total Time off Nest (min) | | | | | |
| | Habitat Type | -0.05 ± 0.06 (grass) | 1,59 | 0.60 | 0.44 |
| | Female Body Condition | 0.02 ± 0.01 | 1,161 | 3.32 | 0.07 |
| | Year | -0.07 ± 0.04 (2017) | 1,160 | 2.76 | 0.10 |

**1** Each variable's coefficient estimates (unstandardized) were obtained using the "summary" function in R and the degrees of freedom, $F/\chi^2$, and *P*-values were obtained using the "anova" function for LMMs and the "Anova" function for GLMs. For categorical variables, the coefficient is calculated for the category in parentheses to compare to the intercept (the category of the variable not indicated in parentheses).

**Table 3.4.** Models for quality of mountain bluebird nestlings in clearcut and grassland habitats in central British Columbia. The colour models are LMs while the rest are LMMs. Immune response is the difference in wing web thickness (mm) 24 hours after a PHA solution injection. Significant *P*-values from the models are bolded.

| Dependent Variable | Model | Coefficient[1] ± SE | DF | *F* | *P* |
|---|---|---|---|---|---|
| Fledging Mass | | | | | |
| | Habitat Type | 1.04 ± 0.40 (grass) | 1,84 | 6.8 | **0.01** |
| | Sex | 0.71 ± 0.19 (male) | 1,425 | 14.5 | **<0.001** |
| | Year | 0.13 ± 0.25 (2017) | 1,463 | 0.3 | 0.61 |
| Wing Length | | | | | |
| | Habitat Type | -1.35 ± 1.03 (grass) | 1,66 | 1.7 | 0.19 |
| | Sex | 0.92 ± 0.41 (male) | 1,352 | 4.9 | **0.027** |
| | Female Parent Age | -2.96 ± 0.90 (yearling) | 1,143 | 10.9 | **0.001** |
| | Nestling Age | 2.25 ± 0.31 | 1,173 | 51.7 | **<0.001** |
| | Year | -1.54 ± 0.73 (2017) | 1,277 | 4.5 | **0.034** |
| Hue (nm) - Females | | | | | |
| | Habitat Type | -6.55 ± 2.68 (grass) | 1,94 | 6.0 | **0.016** |
| | Year | 2.41 ± 2.67 (2017) | 1,93 | 0.8 | 0.37 |
| Brightness - Females | | | | | |
| | Habitat Type | -0.47 ± 0.39 (grass) | 1,94 | 1.4 | 0.24 |
| | Year | -0.20 ± 0.39 (2017) | 1,93 | 0.3 | 0.61 |
| Hue (nm) - Males | | | | | |
| | Habitat Type | 5.12 ± 8.96 (grass) | 1,97 | 0.6 | 0.45 |
| | Year | -21.46 ± 8.98 (2017) | 1,96 | 5.7 | **0.018** |
| Brightness - Males | | | | | |
| | Habitat Type | -0.11 ± 0.39 (grass) | 1,97 | <0.1 | 0.87 |
| | Age | 0.35 ± 0.16 | 1,96 | 5.0 | **0.028** |
| | Year | 0.09 ± 0.42 (2017) | 1,95 | <0.1 | 0.82 |

| Dependent Variable | Model | Coefficient[1] ± SE | DF | *F* | *P* |
|---|---|---|---|---|---|
| Immune Response | | | | | |
| | Habitat Type | 0.02 ± 0.03 (grass) | 1,40 | 0.4 | 0.53 |
| | Mass | 0.01 ± 0.004 | 1,83 | 8.0 | **0.006** |
| | Year | -0.06 ± 0.02 (2017) | 1,83 | 7.3 | **0.009** |

[1] Each variable's coefficient estimates (unstandardized) were obtained using the "summary" function in R and the degrees of freedom, F, and *P*-values were obtained using the "anova" function. For categorical variables, the coefficient is calculated for the category in parentheses to compare to the intercept (the category of the variable not indicated in parentheses).

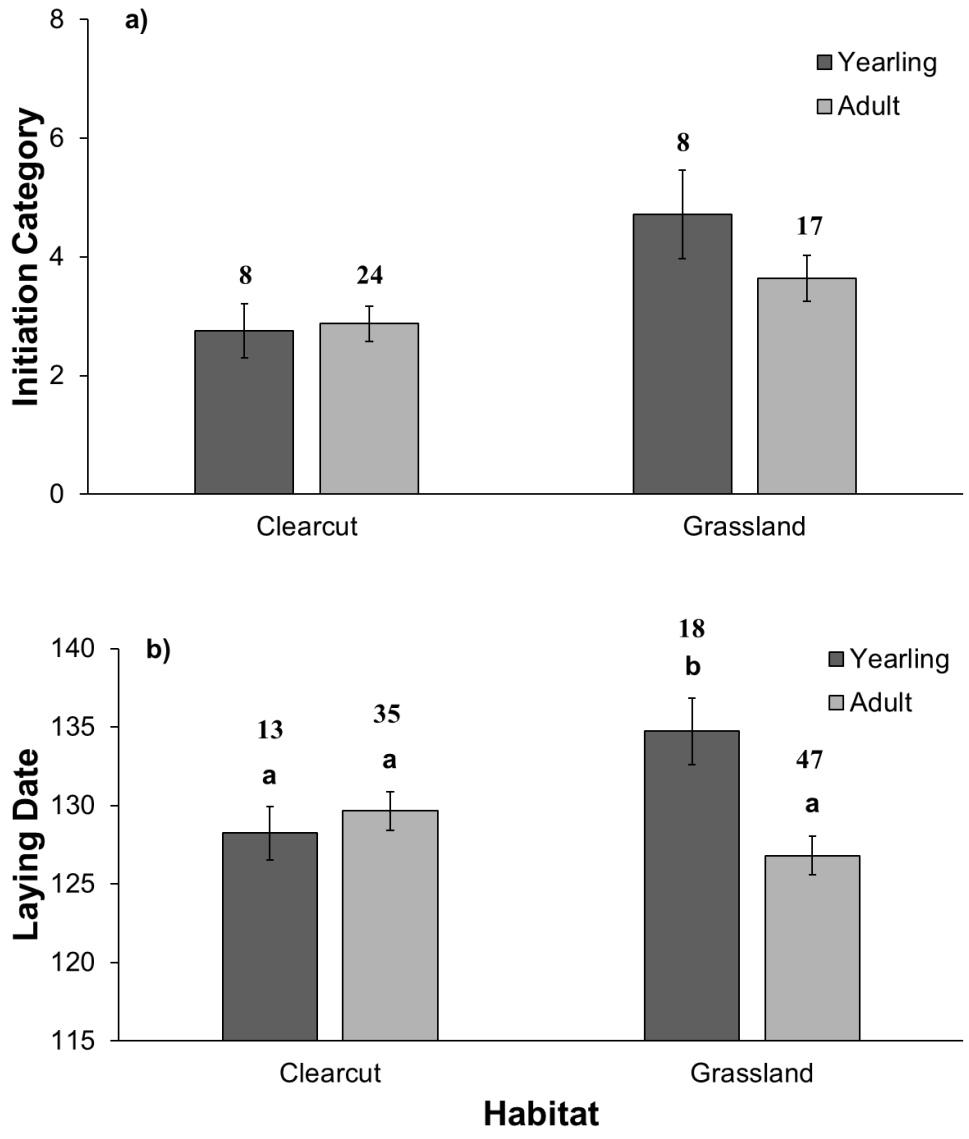


**Figure 3.1.** a) Initiation of nest building by yearling and adult (≥ 2 years old) mountain bluebirds in clearcut and grassland habitats. The initiation categories include five days each, starting with Category 1 having Julian dates 105-110. Category 8 included Julian dates 141-145. The error bars are standard error. The sample sizes are above the columns. b) The average laying dates ± SE for yearling and adult mountain bluebirds. The letters indicate if the habitats are significantly different within an age ($P < 0.05$). The sample sizes are above the columns.

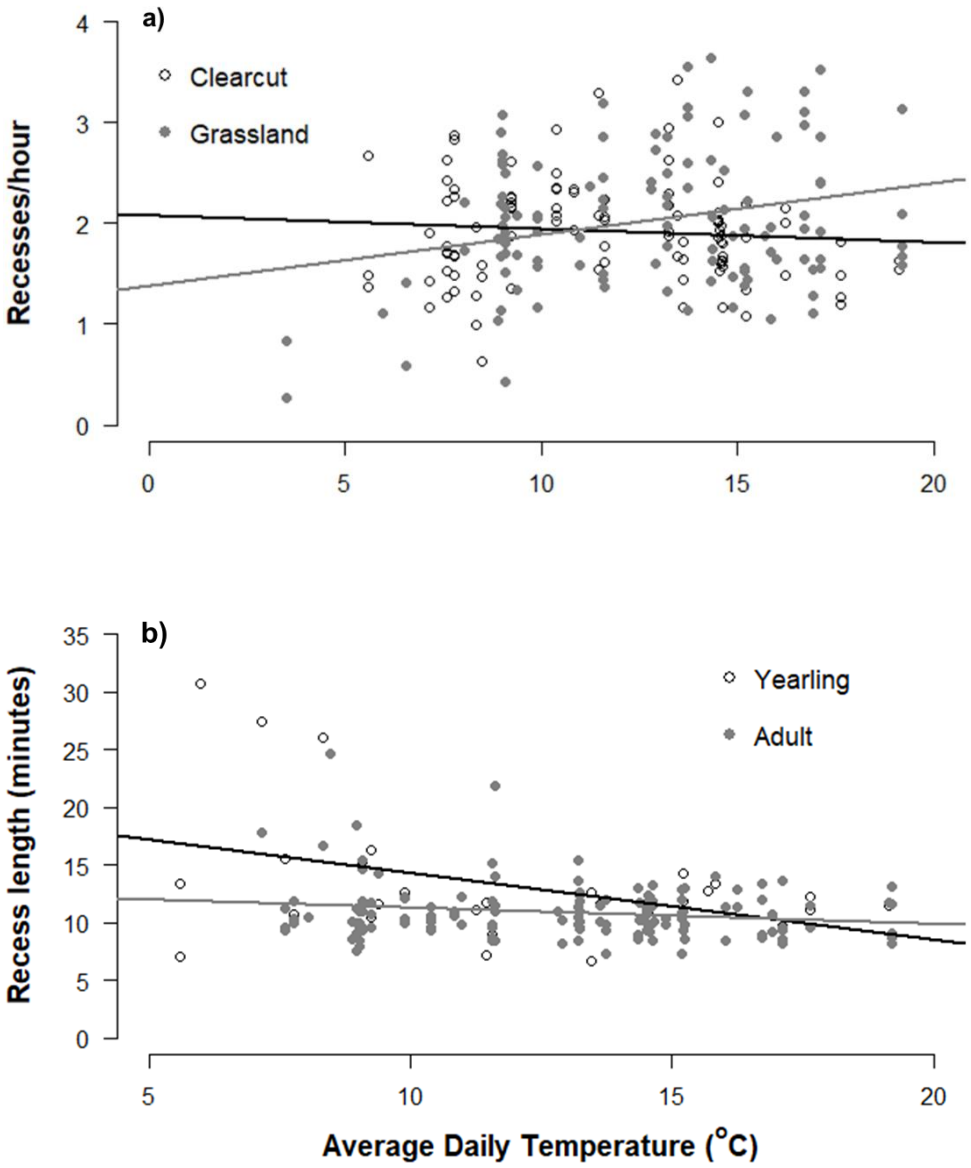


**Figure 3.2.** a) The interaction between habitat type and average daily temperature on the average number of incubation recesses that a mountain bluebird female took each hour. The grey trend line shows the grassland relationship while the clearcut trend line is black. There were 37 nests with incubation data for clearcuts and 41 nests for grasslands. b) The interaction between female age and average daily temperature on the average incubation recess length for mountain bluebirds. The grey trend line shows the adult relationship while the yearling trend line is black. There were 12 nests with incubation data for yearlings and 51 nests for adults.

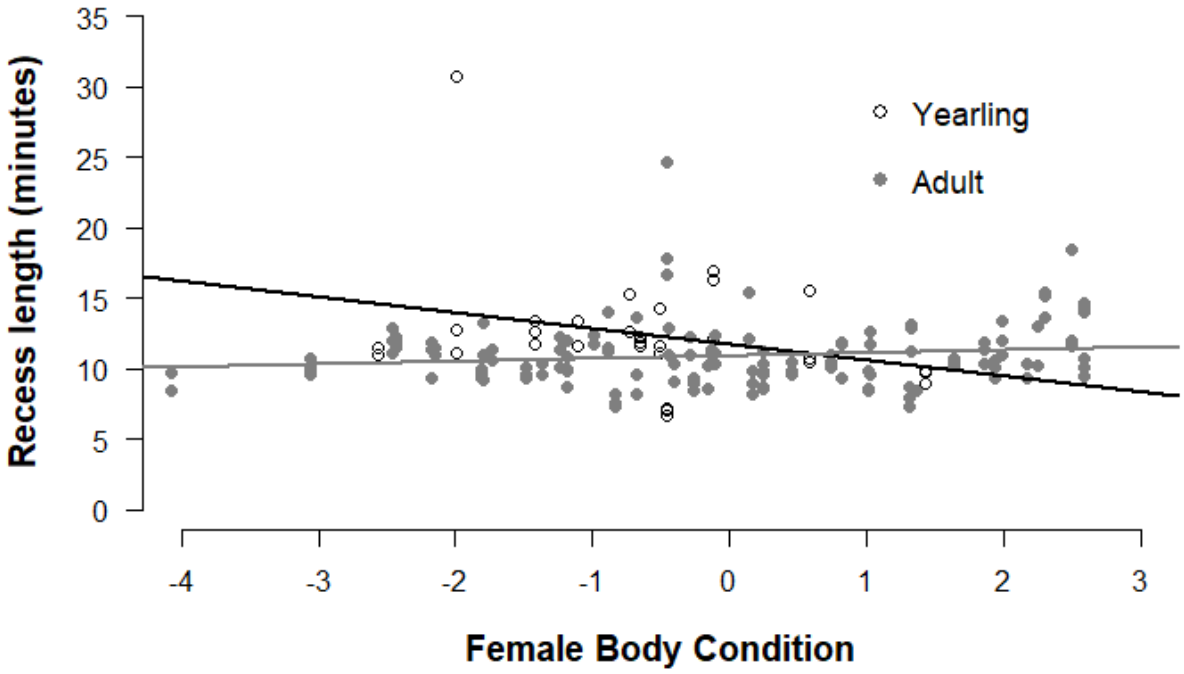


**Figure 3.3.** The interaction between female age and female body condition on the average incubation recess length for mountain bluebirds. The grey trend line shows the adult relationship while the yearling trend line is black. There were 12 nests with incubation data for yearlings and 51 nests for adults.

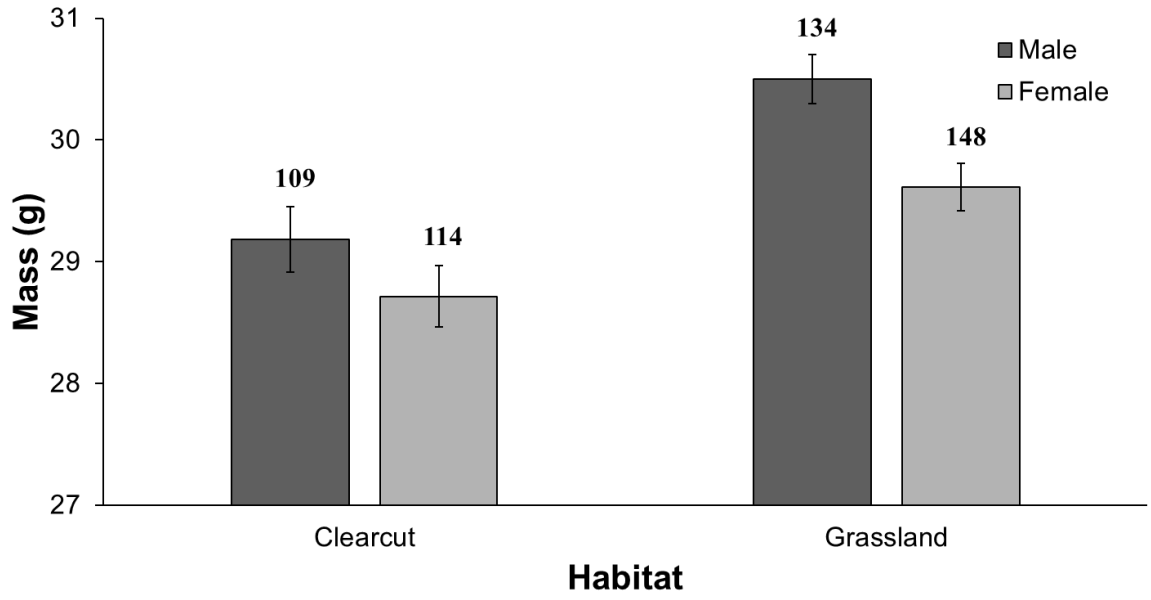


**Figure 3.4.** Mountain bluebird fledgling mass in clearcut and grassland habitats separated by sex. The error bars are standard error. The number of fledglings weighed is shown above the columns. There were 49 clearcut boxes and 65 grassland boxes.

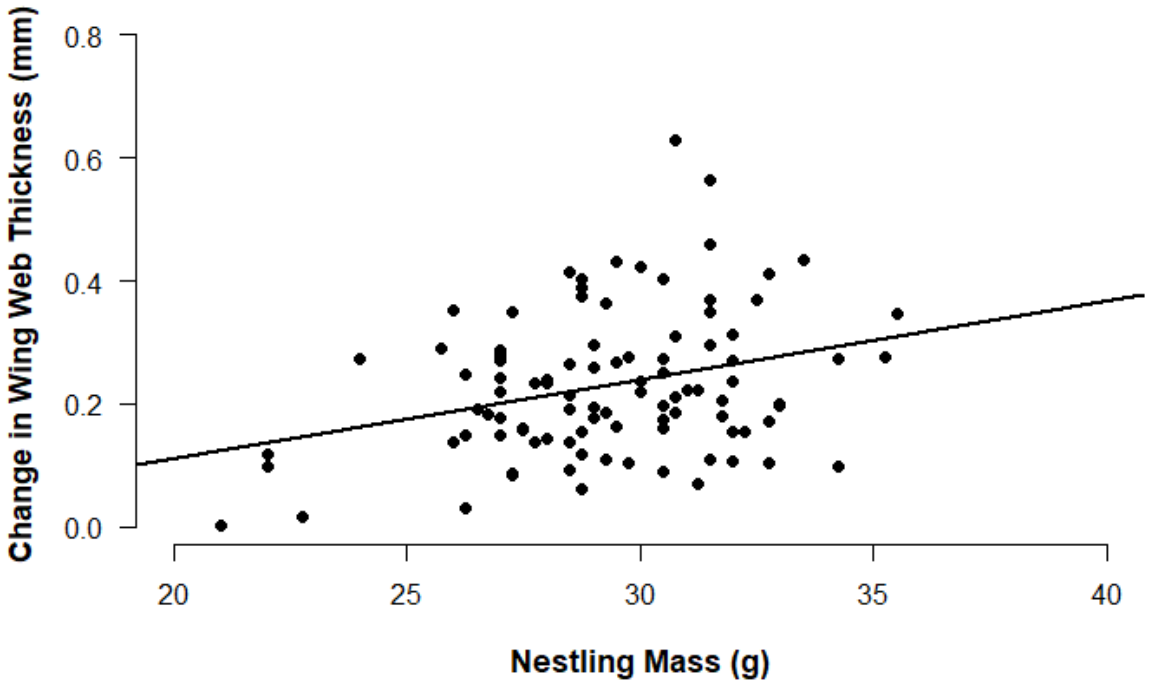


**Figure 3.5.** The relationship between mass of nestling Mountain Bluebirds and T-cell mediated immune response (change in wing web thickness) after injection of phytohemagglutinin (PHA). The trend line shows the pattern for all nestlings (not separated by habitat). There were 101 nestlings measured when 13 days old.

# CHAPTER 4: PREY SIZE AND ITS RELATIONSHIP TO ALLOCATION WITHIN BROODS OF THE MOUNTAIN BLUEBIRD: A TEST OF THE GAPE SIZE CONSTRAINT HYPOTHESIS

## 4.1 Introduction

When incubation begins before clutch completion, nestlings hatch over a span of one or more days. A pattern of such hatching asynchrony, when one or two eggs hatch later than the others in the clutch, is common in passerines, and this difference in nestling age can result in the youngest nestling having reduced growth compared to its older siblings (Soley et al. 2011; Podlas and Richner 2013), which could lead to death or a lower fledging mass (Maddox and Weatherhead 2008; Kim et al. 2010). There are many hypotheses regarding hatching asynchrony, some of which argue it has an adaptive significance, whereas others suggest it is merely the result of energy constraints during incubation (reviews in Magrath 1990; Stenning 1996, Stoleson and Beissinger 1997) and the early death of the smallest nestling is an unintended side-effect.

Regardless of whether hatching asynchrony is adaptive or not for avian parents, the gape size of a nestling limits the size of prey that it can swallow (Wiebe and Slagsvold 2012a). Junior nestlings within broods can be disadvantaged when their parents bring larger prey more suitable for the larger, older nestlings in asynchronous broods (Slagsvold and Wiebe 2007; Wiebe and Slagsvold 2012a). Observations show that some passerine parents attempt to place a prey item into a nestling's mouth but withdraw it when the nestling does not swallow (Glassey and Forbes 2003), and this "testing" increases for insect prey with long wings or legs, perhaps due to the prey item being too large or cumbersome (Slagsvold and Wiebe 2007). Prey items that are tested but not fed to small nestlings are often subsequently given to an older nestling that can swallow the prey, which may intensify the disadvantage of the smallest nestling. However, as nestlings grow, gape size becomes less of a constraint (García-Navas et al. 2012).

Parents of many bird species give food to the largest offspring first (Smiseth et al. 2003; Mainwaring et al. 2011; Wiebe and Slagsvold 2012b), possibly because the larger offspring is more competitive, allowing it to push aside its siblings in the nest to be closest to the parent

(Slagsvold and Rohwer 2000). However, sometimes the food allocation behaviour differs between males and females, with males feeding larger offspring and females evenly distributing food or prioritizing small nestlings (Budden and Beissinger 2009). For example, blue tit (*Cyanistes caeruleus*) nestlings move towards the male who usually feeds the closest nestling, whereas the female distributes food to nestlings farther away from herself, allowing smaller or less competitive nestlings to eat as well (Dickens and Hartley 2007). Female blue tits also feed more spiders (high-quality prey item) to their junior nestlings compared to the older ones, which could help the younger nestlings grow more quickly (García-Navas et al. 2014). Therefore, if females are attuned to their broods' needs, they may reduce the chance of younger nestlings dying before fledging if they have access to a sufficient amount of smaller, more nutritious prey in the habitat. Accordingly, the chance of the junior nestling surviving might depend not only on the total amount of prey available, but also on the size and nutritional quality of the items.

I examined the effect of prey volume and prey type on food allocation within broods of mountain bluebirds (*Sialia currucoides*). The effect of gape size constraints on testing and allocation of insect prey has only been examined in very small passerines, blue tits (Slagsvold and Wiebe 2007, García-Navas et al. 2012) and pied flycatchers (*Ficedula hypoleuca*; Wiebe and Slagsvold 2009), so I wanted to determine whether the constraint was relevant for slightly larger thrush species. I was also interested in whether any differences in diet between those bluebirds in anthropogenically created clearcut habitats versus grassland habitats contributed to different patterns of mortality in broods according to habitat type. I predicted that larger, bulkier food items such as grasshoppers, beetles, and flies would be more difficult for nestlings (especially small nestlings) to swallow and would be tested more often than softer prey items like larvae and spiders. I expected that younger nestlings would die sooner in broods with a high frequency of testing. I predicted that female parents would direct prey to the smaller nestlings in asynchronous broods more than the males, and hence would not always feed the largest or most aggressively begging nestling closest to the entrance hole.

The position of parents at the box when they feed nestlings can also influence food allocation, because parents that fully enter the box are more capable of circumventing large and aggressive nestlings begging at the box entrance (Ryser et al. 2016). Western bluebirds (*Sialia mexicana*) fed nestlings according to intensity of begging, which in turn were the hungrier nestlings, not necessarily the largest ones (Smith et al. 2017). However, entering the box to

distribute food to reduce the effects of competition between nestlings takes longer than feeding from the entrance hole (personal observation). If prey is scarce in a habitat (namely clearcuts), parents may sacrifice time spent in the box allocating prey to the hungrier nestlings and instead feed from the entrance hole. To my knowledge, no one has tested that feeding from the entrance hole is a strategy to increase delivery rates.

## 4.2 Methods

### *4.2.1 Study Site and Study Species*

I studied mountain bluebirds at three study sites in central British Columbia during the breeding seasons of 2016 and 2017. Clearcut and grassland sites were located near Bridge Lake (51° 28' N, 120° 43' W, 1140 m a.s.l.) and grassland sites were located near 100 Mile House (51° 38' N, 121° 17' W, 970 m a.s.l.) and Riske Creek (51°58’ N, 122° 31’ W, 986 m a.s.l.). Over 300 plywood nestboxes were placed on trees in logging cuts that were between 10-45 ha in size and 1-6 years old, and on fenceposts in grazed grasslands that contained native and introduced grasses and forbs. All boxes were at least 400 m apart. The clearcuts were originally mixed forests that included Douglas fir (*Pseudotsuga menziesii*), trembling aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), and white and hybrid spruce (*Picea glauca* and *P. glauca* X *engelmannii*).

The mountain bluebird is an insectivorous cavity-nesting thrush that readily settles in clearcuts despite its natural habitat being grasslands (Holt and Martin 1997). After migration, mountain bluebirds begin to settle on the study area around mid-April and lay clutches of 5-6 eggs on average. Broods are relatively synchronous but “runt” nestlings are not uncommon, meaning incubation can start with the penultimate egg (Power and Lombardo 1996). Both sexes provision the offspring with a variety of invertebrate prey, including Lepidoptera (adults and larvae), Arachnida, Coleoptera, Orthoptera, and Hymenoptera (Power 1980; Herlugson 1982), and the nestlings fledge after 15-22 days (Johnson et al. 2013a).

### *4.2.2 Field Work*

Once nestlings hatched, adults were captured using swing-door traps over the entrance hole to the box and were banded with a unique combination of aluminum and plastic colour bands (n=123 in 2016, 94 in 2017). Birds were aged as adults versus yearlings based on molt (Pyle 1997), were weighed, and were measured according to six structural sizes: head-bill, 9th primary, central rectrix, tarsus, culmen, and flattened wing chord. These measures were used to

calculate a single size variable in a principal component analysis (one for each sex). I used the score on the first axis (PCA1) as a measure of body size (Rising and Somers 1989), and I calculated body condition as the residuals of a regression of body mass on PCA1 (Labocha and Hayes 2012; Wiebe and Vitousek 2015). Nestboxes were visited every 4-5 days to record nestling survival, and all nestlings were weighed before each filming period or at least three times during the nestling period.

I placed microcameras (either GOPROs or custom-built motion-triggered digital mini cameras) in the ceiling of a nestbox to film parental deliveries during 3-hour filming blocks. Using the films of parental deliveries, I recorded the length and the width of the prey item using the bill of the adult as a known size. Prey volume was calculated using the equation of a cylinder: $\pi$ $(0.5\text{width})^2$*length (Slagsvold and Wiebe 2007). I also recorded whether parents tested a nestling when they placed the item into a gape and which nestling swallowed the prey. Parents always entered the box to feed nestlings when they were young, but at the older stages, I also recorded if the parents fed their nestlings while standing in the entrance hole instead of fully entering the nestbox. Information on testing and entrance hole feeding was available for each filming event (n = 166 filming periods at 41 boxes in grasslands and 51 boxes in clearcuts). The number of provisioning visits recorded during filming bouts ranged from 1-90 (mean 26).

To determine if the youngest nestling in asynchronous broods was disadvantaged by its relatively small gape size during the early stage of nestling development (Day 0-4), I marked its head with a small dot of white liquid paper to identify it in the video tapes and see whether it was offered, and ate, prey items. I did not quantify begging because nestlings only raise their heads and gape at this age. Nestlings were not marked in synchronous broods in which there was no small nestling that was measurably less in mass than the others. Sample size at the early nestling stage with a marked nestling was 5 clearcut and 7 grassland boxes in 2016 and 19 clearcut and 9 grassland boxes in 2017. In addition to the young nestling stage, I tried to film nestboxes two more times as nestlings aged (between 5-15 d old) on days with no rain, but poor weather or failures of cameras meant the same broods were filmed only once with older nestlings. The sample size of filming bouts for all older nestlings was 47 films at 19 clearcut boxes and 19 grassland boxes in 2016, and 56 films at 20 clearcut and 15 grassland boxes in 2017.

*4.2.3 Statistical Analyses*

I used R version 3.4.3 (R Core Team 2017) and report data as means ± standard error in the results section, unless indicated otherwise. Initial models included two-way interactions but during model simplification they were eliminated if non-significant ($\alpha > 0.05$). The models' remaining explanatory variables are in Table 4.1 and 4.2. I ran an LMM to determine if hatching asynchrony (difference in mass between the largest and smallest nestling within a brood when 0-4 d old) was affected by habitat type, brood size, laying date, female body condition, female age, and year (library "lmerTest", Kuznetsova et al. 2017). The random effect was nestling age, since differences in mass might vary slightly with age of measurement. I log-transformed hatching asynchrony to make the data have a normal distribution.

I did several GLMMs and GLMs using a binomial distribution to analyze testing and food allocation in clearcut and grassland habitats, obtaining *P*-values using the R library "car" and the function "Anova" (Fox and Weisberg 2011). The random effect was nestbox in each model. The testing model originally had brood size, nestling stage (early (0-4 d old), middle (5-11 d old), and late (≥ 12 d old)), prey volume (log-transformed), prey type, parent sex, and year as fixed effects. Only visits in which parents fed from inside the box were included in the testing model and the sex of the parent was the one that placed prey in the nestlings' gapes, since males passed food to the female often during the early nestling stage as the female brooded. I also analyzed testing in the early nestling stage to examine trends at a finer scale with habitat type, brood size, nestling age, prey volume (log-transformed), prey type, parent sex, and year as fixed effects. To determine if the smallest nestling was tested or fed a certain prey item (yes versus no), I did two GLMMs for broods in the early nestling stage, using brood size, nestling age, prey volume (log-transformed), prey type, parent sex, and year as fixed effects. I ran a GLMM to determine if parents differed in offering the smallest nestling a prey item first using habitat type, brood size, prey volume (log-transformed), prey type, parent sex, and year as fixed effects. I also analyzed whether the smallest nestling in early-stage broods was tested and then fed, or if a larger nestling was tested and then the smallest nestling was fed using GLMMs with habitat type, brood size, nestling age, prey volume (log-transformed), prey type, parent sex, and year as fixed effects.

To determine if testing affected fledging success, I calculated the proportion of prey that was tested during the filming bout for each box in the early nestling stage, and used this, habitat

type, hatching asynchrony (difference in mass between the largest and smallest nestling), and year as explanatory variables in a GLM testing fledging success (proportion of the brood that fledged excluding nests that failed completely). I also did a GLM where broods were categorized as either fledging all young or one or more nestlings dying (not all) with the same variables.

I ran a chi-square test comparing the number of nests that fledged all their nestlings versus boxes that did not fledge 100% (but fledged at least one nestling) between habitats. This test was conducted on first nesting attempts only. I ran a GLMM to determine if parents fed from the entrance hole or entered the box, including habitat type, brood size, nestling stage, parent sex, and year as the fixed effects and nestbox as the random effect. I used two GLMs to test if feeding from the entrance hole in either the middle or late nestling stage affected fledging success in nestboxes that fledged at least one individual. The explanatory variables were habitat type, the proportion of feeding events that took place in the entrance hole, and year. I also did two GLMs where broods were categorized as either fledging all young or one or more nestlings dying with the same variables. Finally, I did two LMMs (one for the middle nestling stage and one for the late nestling stage) on delivery rates with parent sex, proportion of feedings from the entrance hole, and year as the fixed effects and nestbox as the random effect.

## 4.3 Results

### *4.3.1 Hatching Asynchrony and Brood Size*

The mean difference in mass between the largest and smallest nestling within broods was 1.9 g $\pm$ 0.2 and it did not differ between habitats, brood size, or year but increased slightly with laying date (LMM: habitat effect, $F_{1,71} = 0.88$, $P = 0.35$; brood size: $F_{1,72} = 2.80$, $P = 0.10$; year: $F_{1,74} = 0.41$, $P = 0.53$; laying date $F_{1,72} = 5.71$, $P = 0.019$;). The degree of hatching asynchrony was not related to any female characteristics. Brood size (n = 83) averaged 5.0 $\pm$ 0.1 (range 2-7) across all boxes, but it was not significant in any model of testing or food allocation, and so, for simplicity, it was removed as a factor in all subsequent models.

### *4.3.2 Testing*

A GLMM with just habitat type as a fixed factor found no significant difference between habitats in the proportion of feeding events that included testing ($\chi^2_1$=0.04, $P$=0.84), and habitat type was not significant in any other model of provisioning when prey volume and size were included; and so, for simplicity, habitat was eliminated from subsequent testing models. However, testing increased as prey volume increased (Table 4.1). Regarding prey type, I

discovered that all prey types were tested equally (28% of 3,205 of items). There were no differences in testing between sexes at any stage (interaction: $\chi^2_2$=1.21, *P*=0.55) but testing decreased as nestlings aged (Figure 4.1). I also checked if the sex that delivered the prey item (as opposed to the one that actually fed the nestling) affected testing but I found that there was still no significant difference in testing between sexes (GLMM: $\chi^2_1$<0.01; *P*=0.98). Since I am more interested in which nestling the parent was directing the prey to, I used the parent that actually tested and fed nestlings in subsequent models.

Testing of nestlings at the youngest stage (n = 63 boxes) decreased as nestlings aged (Table 4.1; Figure 4.2) and declined rapidly for nestlings more than 1 d old. Prey volume was positively associated with the likelihood of testing (Figure 4.3) and prey type also affected the probability of testing at this early stage (although not quite significant), with spiders and larvae being the prey types tested at different rates (Tukey test; library "multcomp", Hothorn et al. 2008). Differences in the magnitude of testing among prey types was small, however, since on average 0.44 $\pm$ 0.02 of spiders were tested relative to 0.40 $\pm$ 0.02 of larvae.

Across both habitats, the overall proportion of feeding events during which the smallest nestling was tested was 0.16 $\pm$ 0.01 and this was the same frequency that the smallest nestling was fed the prey item. Testing of the smallest nestling decreased with increasing nestling age (although not quite significant; Table 4.1), but the proportion of feeding events fed to the smallest did not change with nestling age. The smallest nestling was fed less often after a nestling was tested (either the smallest or a larger nestling) when the prey item was larger, although this relationship was not quite significant when a larger nestling was tested first (Table 4.1; Figure 4.4). However, when the smallest nestling was tested with a small prey item, parents were more likely to feed the smallest nestling instead of transferring the prey item to a larger nestling. Smaller nestlings were fed more often after a larger nestling was tested when the nestlings were older, but this pattern was not seen when the smallest nestling was tested first. With respect to who parents first offered the prey item, the smallest nestling was the first target of 19% of provisioning visits, but this did not differ between parents ($\chi^2_1$=0.33; *P*=0.57) or year ($\chi^2_1$=0.22; *P*=0.64).

*4.3.3 Nestling Mortality and Patterns of Feeding*

Excluding broods that failed completely as a result of abandonment or depredation and considering only first nesting attempts, 28.9% of 38 broods in clearcuts and 24.1% of 58 broods

in the grasslands experienced the mortality of at least one nestling and this proportion did not differ between habitats (chi-square test, $\chi^2_1$ =0.08, $P$ = 0.77). If mortality of nestlings occurred, typically only 1 nestling died (12.5% of 96 broods that fledged at least one young) although a few broods had two (7.3%) or three (6.3%) nestlings die (Figure 4.5). Most of the nestlings died in the late nestling stage (older than 11 days), although I was only able to sex 7 nestlings when they died: 3 were male and 4 were female.

The proportion of the brood that fledged was not affected by the proportion of prey that were tested during the early nestling stage (GLM, $\chi^2_{1,44}$= 1.40, $P$ = 0.24), habitat ($\chi^2_{1,45}$= 1.12, $P$= 0.29), hatching asynchrony ($\chi^2_{1,43}$= 1.93, $P$ = 0.16), or year ($\chi^2_{1,42}$= 1.19, $P$ = 0.28). Similarly, when broods were categorized as either fledging all young versus having one or more nestlings dying, there was no difference based on habitat ($\chi^2_{1,45}$= 0.76, $P$ = 0.38), testing ($\chi^2_{1,44}$= 0.70, $P$= 0.40), hatching asynchrony ($\chi^2_{1,43}$= 0.36, $P$ = 0.55), or year ($\chi^2_{1,42}$= 1.53, $P$ = 0.22).

The earliest nestling age that parents started feeding from the hole was 1 d old (only once at two grassland boxes). The earliest nestling age that parents started feeding from the entrance hole in clearcuts was 6 d old. Films from inside the box during the late nestling stage confirmed that usually nestlings were sleeping when a parent landed in the entrance hole, and in response to the noise, nestlings stretched their necks towards the parent immediately, jostling their siblings. The likelihood of parents feeding from the entrance hole did not vary with brood size or with habitat type but occurred more often in later nestling stages than earlier nestling stages (Table 4.2; Figure 4.6). The habitat * parent sex interaction resulted from females feeding from the entrance hole less often than males in grasslands (Figure 4.6). The frequency of feeding from the entrance hole was not associated with fledging success in the brood (Table 4.2). When broods categorized either fledging all young versus having one or more nestlings dying (not all), there was no difference based on habitat type (middle stage: $\chi^2_{1,69}$= 0.04, $P$ = 0.84; late: $\chi^2_{1,25}$= 2.48, $P$ = 0.12) or feeding from the entrance hole (middle: $\chi^2_{1,68}$= 0.11, $P$ = 0.74; late: $\chi^2_{1,24}$= 0.30, $P$= 0.58). Feeding from the entrance hole did not affect delivery rates during the middle nestling stage but increased entrance feeding was associated with increased delivery rates in the late nestling stage (Table 4.2).

**4.4 Discussion**

Similar to the pattern found in smaller passerines (Slagsvold and Wiebe 2007; Wiebe and Slagsvold 2012a), testing of prey was most frequent when nestlings were very young, and

increased with increasing prey volume, supporting the gape size constraint hypothesis. However, junior nestlings in mountain bluebird broods, while they were fed less with large prey, did not appear to be strongly disadvantaged, as fledging success was not associated with the frequency of testing during the early nestling stages. Perhaps because the degree of hatching asynchrony in broods was small, the skew of provisioning was not strong enough to result in many young nestlings starving in either habitat. Hatching asynchrony was not different between the two habitats, and since incubation behaviour in mountain bluebirds affects the degree of hatching asynchrony (Johnson et al. 2013b), it is likely that incubation onset was also similar in clearcuts and grasslands.

*4.4.1 Testing*

Consistent with predictions of gape size constraints on swallowing ability (Slagsvold and Wiebe 2007), several variables were correlated with the likelihood of testing in bluebird broods. Nestlings were tested more often as prey volume increased, both when measured across the entire nestling period and within the earliest nestling stage. The proportion of feeding events that involved testing decreased as the nestlings got older and their gape sizes increased, which is also seen in blue tits (García-Navas et al. 2014).

Testing decreased across the three stages of the nestling period and within the youngest nestling stage as the nestlings grew. Hence, the most critical bottleneck for gape size constraints in mountain bluebirds occurred within the first 4 days (early nestling stage) and especially within the first two days after hatch. Power and Lombardo (1996) suggest that late-hatched mountain bluebird nestlings may be able to catch up to their older siblings regarding growth within one day of hatching. In pied flycatchers, rates of testing decreased substantially in the first four days as well (Slagsvold and Wiebe 2007). The mortality of junior nestlings in asynchronous broods often occurs when nestlings are quite young (Granbom and Smith 2006; Slagsvold and Wiebe 2007; Mock et al. 2009). In contrast, most nestling mortality in my study occurred in the late nestling stage, probably because most broods were fairly synchronous, and perhaps food was not limiting until later in the nestling stage. The relatively high energy demands of older insectivorous nestlings may also trigger mortality at that stage if cold weather impedes provisioning, like in tree swallows (*Tachycineta bicolor*) (Winkler et al. 2013). Therefore, the mountain bluebirds in my study probably did not have a high degree of asynchrony so brood reduction did not occur in the early nestling stage.

Although female mountain bluebirds on average brought smaller prey than males (Chapter 2), the sexes had similar rates of testing. This pattern was complicated by the fact that, especially during the early nestling stage, the males passed prey items to the female when she was brooding (personal observation) and then she tested the nestlings. However, there was no difference in testing based on which parent brought the prey item. Therefore, the prey size differences between parent sexes may not be large enough to result in differences in testing behaviour.

In the early nestling stage, the only prey types that had different rates of testing were spiders and larvae, with more testing of the former. These were the most common prey of young nestlings, comprising 63% of items, and so the rarity of other prey may have obscured patterns of testing among them. Spiders had long legs, although usually folded into the body, and larvae were more compact but overall differences in testing according to insect taxon were small, so size rather than species of insect seems to be the driving factor.

When a prey item was small, although the smallest nestling might be tested, it was more likely to get the prey item eventually than when the prey was large. This is probably because small items that were tested were not in an optimum position in the parent's bill to feed the nestling but, after repositioning, could then fit into the nestling's gape and be swallowed. In contrast if the item was simply too large to fit, the only option was for the parent to move onto a larger nestling (Wiebe and Slagsvold 2009). Similar to the situation in Slagsvold and Wiebe (2007), there were few instances of prey transferred from large to small nestlings after testing, but this proportion increased when nestlings aged from 0-4 d, as the gapes of all nestlings grew and became more capable of swallowing larger prey. So, the advantage of being a larger, older nestling was short-lived in my study. Females did not allocate more food to the junior nestling compared to males in the early nestling stage in contrast to what some other studies have found (Budden and Beissinger 2009; Ryser et al. 2016), possibly because the degree of asynchrony was not large. However, Wiebe and Slagsvold (2009) found that female pied flycatchers did not allocate more food to junior nestlings over larger nestlings, so preference for feeding smallest nestlings over larger nestmates is not always the case (Mock et al. 2011). The consequences of testing during the early nestling stage did not affect fledging proportions as few junior nestlings died of starvation. Overall, the junior nestlings received sufficient prey that were not too large or too difficult to swallow.

*4.4.2 Position of Parents during Feeding*

Parents fed from the entrance hole more often as nestlings got older as has been found for a few other species like tree swallows (Slagsvold and Rohwer 2000) and Syrian woodpeckers (*Dendrocopos syriacus*; Mersten-Katz et al. 2012). Nestlings closest to the entrance hole get fed more often (Leonard and Horn 1996) and feeding from the entrance hole could mean that the parents were feeding the larger or most competitive nestlings (Kacelnik et al. 1995). Equal food distribution among offspring is not always the goal of avian parents which may prioritize the largest offspring (Smiseth et al. 2003; Mainwaring et al. 2011; Wiebe and Slagsvold 2012b) that may be the highest quality.

The prevalence of feeding from the entrance hole did not differ between habitat types, but, at least in grasslands, the greater propensity of males to feed rapidly and from the entrance compared to females which fully enter the box to spend more time allocating items is a pattern seen in a few other species, including tree swallows (Whittingham et al. 2003) and European hoopoes (*Upupa epops*, Ryser et al. 2016). Budden and Beissinger (2009) found that green-rumped parrotlet (*Forpus passerinus*) males favoured larger, more competitive nestlings while females provisioned the smaller, less competitive nestlings more often than males did. Similarly, male blue tits also fed the closest, more competitive nestling whereas females distributed food more evenly, although this feeding took place within the nestbox (Dickens and Hartley 2007; Dickens et al. 2008). Despite any competition to access the nest box entrance, feeding from the entrance hole did not affect fledging success, so the less competitive nestlings apparently still received adequate food.

Experimental manipulation of food supply is required to test the idea that feeding from the hole was a direct response to foraging demands on the parent. Brood size was not associated with the frequency of feeding from the entrance but if parents adjust clutch and brood size to their own foraging capacity, such trade-offs may be obscured. However, delivery rates increased with increased frequency of feeding from the entrance during the late nestling stage, possibly indicating that feeding from the entrance hole is a time-saving strategy for mountain bluebirds when food demand was highest. Other explanations for feeding from the entrance hole could be that it is a strategy to decrease the risk of predation and parasite infections in the adult (Ryser et al. 2016). Parents may also feed from outside the box simply because of physical constraints of crowding in the box when the nestlings are near fledging. Female Eurasian kestrels (*Falco*

*tinnunculus*) had difficulty entering the nest cavity due to overcrowding later in the nestling period (Steen et al. 2012) and the vigorous pushing and jostling of large tree swallow nestlings tended to block the entrance hole (Slagsvold and Rohwer 2000).

In sum, I found support for the idea that gape size constraints affect food allocation with broods of bluebirds at young nestling ages. Although small nestlings received less prey than larger nestmates because of testing, the skew in food distribution was not large enough to cause increased mortality in these broods, perhaps because the degree of hatching asynchrony, and hence the variance in gape sizes, was small. Neither parent tended to offer prey items first to the smallest nestling and so were not favouring junior nestlings during the early nestling stage. Perhaps, in cases of greater asynchrony, intrabrood differences in gape size persist longer and might result in more deaths of the smallest nestling. However, mountain bluebirds in both clearcuts and grasslands in central British Columbia seemed to have similar degrees of asynchrony and similar feeding patterns, so gape size constraints do not appear to be operating in one habitat type more than the other.

**Table 4.1.** GLMMs for prey testing (placing item in a gape and then withdrawing it) in mountain bluebirds nesting in either clearcut or grassland habitats in central British Columbia. Overall testing refers to testing that happened across all nestling ages, while early stage testing was when nestlings were 0-4 days old. "Smallest" in the model title refers to the lightest nestling in a brood during the early nestling stage. Significant *P*-values are bolded.

| Dependent Variable | Model | Coefficient[1] ± SE | DF | $\chi^2$ | *P* |
|---|---|---|---|---|---|
| Overall Testing | | | | | |
| | Nestling Stage | -1.73 ± 0.13 (middle)<br>-2.65 ± 0.26 (late) | 2 | 202.89 | <**0.001** |
| | Prey Volume | 0.46 ± 0.05 | 1 | 94.03 | <**0.001** |
| | Parent Sex | -0.10 ± 0.09 (male) | 1 | 1.16 | 0.28 |
| | Year | -0.15 ± 0.14 (2017) | 1 | 1.12 | 0.29 |
| Early Stage Testing | | | | | |
| | Nestling Age | -0.61 ± 0.11 | 1 | 29.53 | <**0.001** |
| | Prey Volume | 0.55 ± 0.08 | 1 | 51.89 | <**0.001** |
| | Parent Sex | 0.01 ± 0.13 (male) | 1 | 0.002 | 0.96 |
| | Prey Type | -1.24 ± 1.26 (larva)<br>-0.59 ± 1.25 (spider) | 13 | 21.81 | 0.058 |
| | Year | -0.21 ± 0.22 | 1 | 0.95 | 0.33 |
| Tested Smallest | | | | | |
| | Nestling Age | -0.34 ± 0.18 | 1 | 3.42 | 0.06 |
| | Prey Volume | 0.22 ± 0.10 | 1 | 4.86 | **0.027** |
| | Parent Sex | 0.01 ± 0.21 (male) | 1 | 0.003 | 0.96 |
| | Year | 0.16 ± 0.31 (2017) | 1 | 0.27 | 0.60 |
| Fed Smallest | | | | | |
| | Prey Volume | -0.17 ± 0.08 | 1 | 4.08 | **0.043** |
| | Parent Sex | 0.06 ± 0.20 (male) | 1 | 0.09 | 0.76 |
| | Year | 0.02 ± 0.20 (2017) | 1 | 0.01 | 0.91 |

| Dependent Variable | Model | Coefficient[1] ± SE | DF | $\chi^2$ | *P* |
|---|---|---|---|---|---|
| Tested and Fed Smallest | | | | | |
| | Nestling Age | 0.26 ± 0.25 | 1 | 1.10 | 0.29 |
| | Prey Volume | -0.43 ± 0.19 | 1 | 5.04 | **0.025** |
| | Parent Sex | -0.13 ± 0.40 (male) | 1 | 0.10 | 0.75 |
| | Year | 0.07 ± 0.40 (2017) | 1 | 0.03 | 0.87 |
| Tested Large and Fed Smallest | | | | | |
| | Nestling Age | 0.84 ± 0.34 | 1 | 6.13 | **0.013** |
| | Prey Volume | -0.49 ± 0.25 | 1 | 3.74 | 0.053 |
| | Parent Sex | -0.05 ± 0.51 (male) | 1 | 0.01 | 0.91 |
| | Year | 0.07 ± 0.51 (2017) | 1 | 0.02 | 0.89 |

**1** Coefficient estimates (unstandardized) were obtained using the "summary" function in R and the degrees of freedom, $\chi^2$, and *P*-values were obtained using the "Anova" function. The coefficient of categorical variables is shown for the category in parentheses in reference to the intercept (the category of the variable not indicated in parentheses), but the other columns refer to the categorical variable as a whole. The prey type row only includes two coefficients instead of 13.

**Table 4.2.** GLMM, GLMs, and LMMs for the frequency that parents fed from the entrance hole versus from inside the box in mountain bluebirds nesting in either grassland or clearcut habitats in central British Columbia. The two GLM models test the effect of entrance hole feeding (EHF) on fledging proportions in the middle and late nestling stage (excluding nests that failed completely). The GLMM and GLMs have $\chi^2$ statistics and the LMMs have F-values. Significant *P*-values are bolded.

| Dependent Variable | Model | Coefficient[1] ± SE | DF | *F* or $\chi^2$ | *P* |
|---|---|---|---|---|---|
| EHF - GLMM | | | | | |
| | Habitat Type | -0.83 ± 0.63 (grass) | 1 | 0.60 | 0.44 |
| | Brood Size | 0.08 ± 0.18 | 1 | 0.19 | 0.66 |
| | Nestling Stage | 6.87 ± 0.84 (middle)<br>9.96 ± 0.88 (late) | 2 | 241.88 | **<0.001** |
| | Parent Sex | 0.06 ± 0.17 (male) | 1 | 18.22 | **<0.001** |
| | Habitat Type * Parent Sex | 0.80 ± 0.23 (grass & male) | 1 | 11.77 | **<0.001** |
| Fledging Proportion - GLM | | | | | |
| | Habitat Type | 0.20 ± 0.36 (grass) | 1,69 | 0.30 | 0.59 |
| | Middle Stage EHF | -0.32 ± 0.59 | 1,68 | 0.29 | 0.59 |
| | Year | 1.60 ± 0.42 (2017) | 1,67 | 17.50 | **<0.001** |
| Fledging Proportion - GLM | | | | | |
| | Habitat Type | -17.97 ± 3.7 x$10^3$ (grass) | 1,25 | 2.31 | 0.13 |
| | Late Stage EHF | 1.12 ± 2.16 | 1,24 | 0.29 | 0.59 |
| | Year | 0.01 ± 1.45 (2017) | 1,23 | <0.001 | 0.99 |
| Delivery Rates - LMM | | | | | |
| | Middle Stage EHF | -0.06 ± 0.99 | 1,125 | 0.003 | 0.95 |
| | Parent Sex | -0.97 ± 0.51 (male) | 1,90 | 3.70 | 0.057 |
| | Year | -0.59 ± 0.59 (2017) | 1,110 | 1.01 | 0.32 |

| Dependent Variable | Model | Coefficient[1] ± SE | DF | $F$ or $\chi^2$ | $P$ |
|---|---|---|---|---|---|
| Delivery Rates - LMM | | | | | |
| | Late Stage EHF | 3.35 ± 1.08 | 1,39 | 9.67 | **0.003** |
| | Parent Sex | -3.05 ± 0.67 (male) | 1,24 | 20.54 | **<0.001** |
| | Year | 0.01 ± 0.86 (2017) | 1,34 | <0.001 | 0.99 |

[1] Each variable's coefficient estimates (unstandardized) were obtained using the "summary" function in R. The degrees of freedom, $\chi^2$, and *P*-values for the GLMM and GLMs were obtained using the "Anova" function while I used the "anova" function to get the degrees of freedom, F, and *P*-values for LMMs. For categorical variables, the coefficient is calculated for the category in parentheses to compare to the intercept (the category of the variable not indicated in parentheses), but the other columns refer to the categorical variable as a whole.

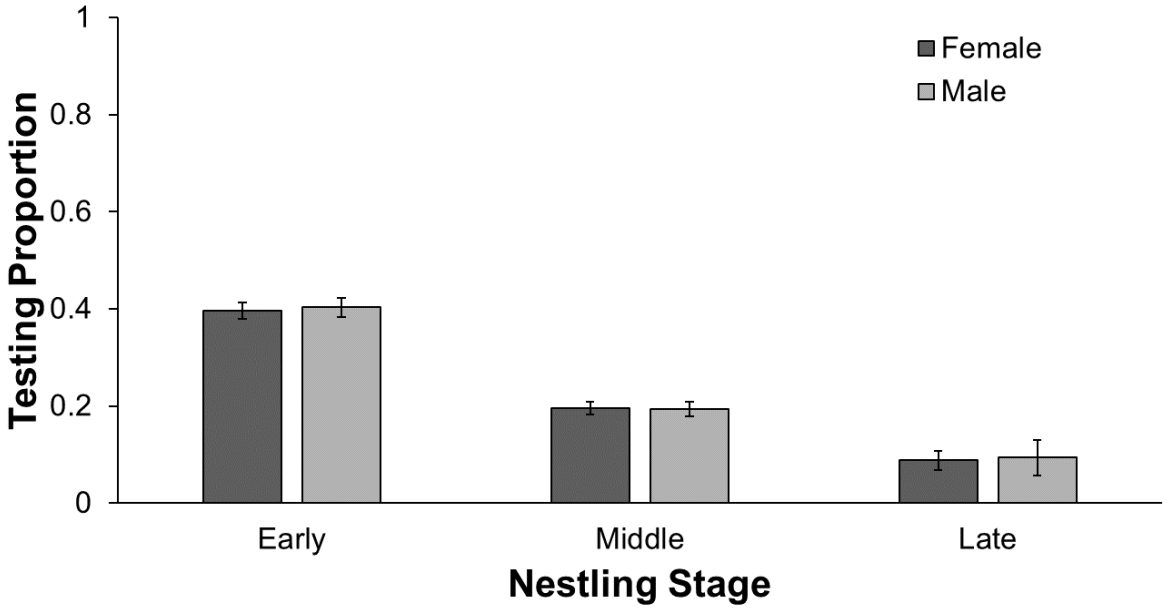


**Figure 4.1.** The proportion of prey items that were tested by male and female mountain bluebird parents in each nestling stage (early: 0-4 d old, middle: 5-11 d old, late: ≥ 12 d old). The error bars are standard error. The number of boxes with filming data was 63 in the early nestling stage, 75 in the middle, and 28 in the late nestling stage.

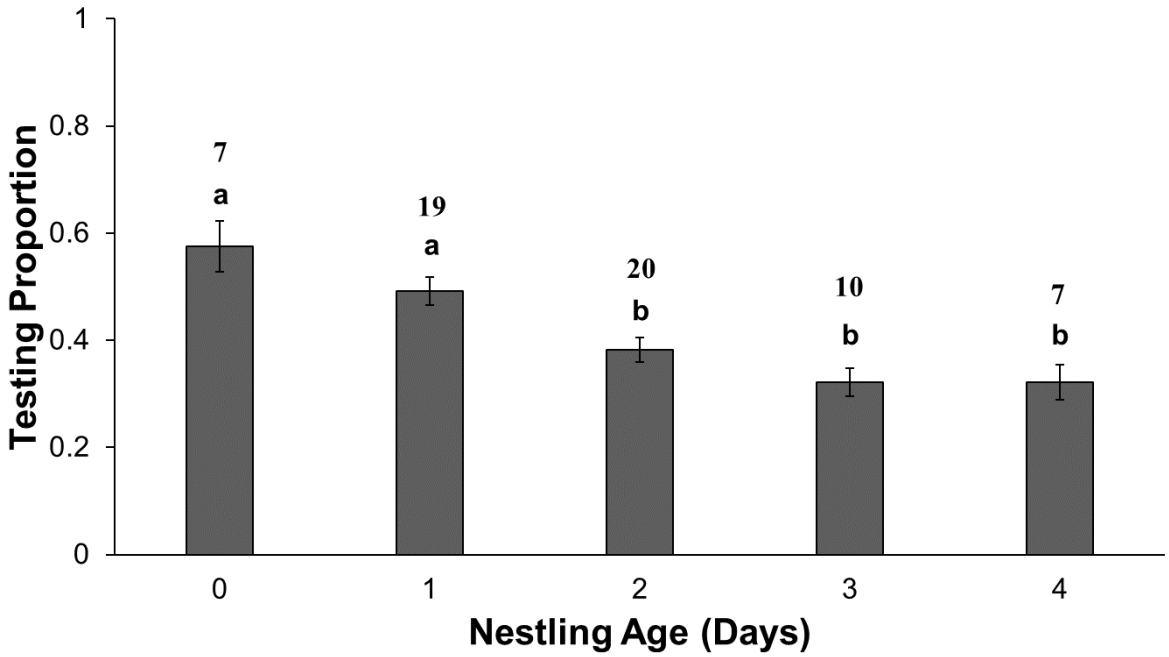


**Figure 4.2.** The effect of nestling age on the average proportion of prey items delivered by mountain bluebird parents that were tested during the early nestling stage. Age 0 is the day of hatching. The error bars are standard error. The letters indicate if the testing proportion was significantly different between nestling ages ($P < 0.05$). The number of boxes with filming data are above the columns.

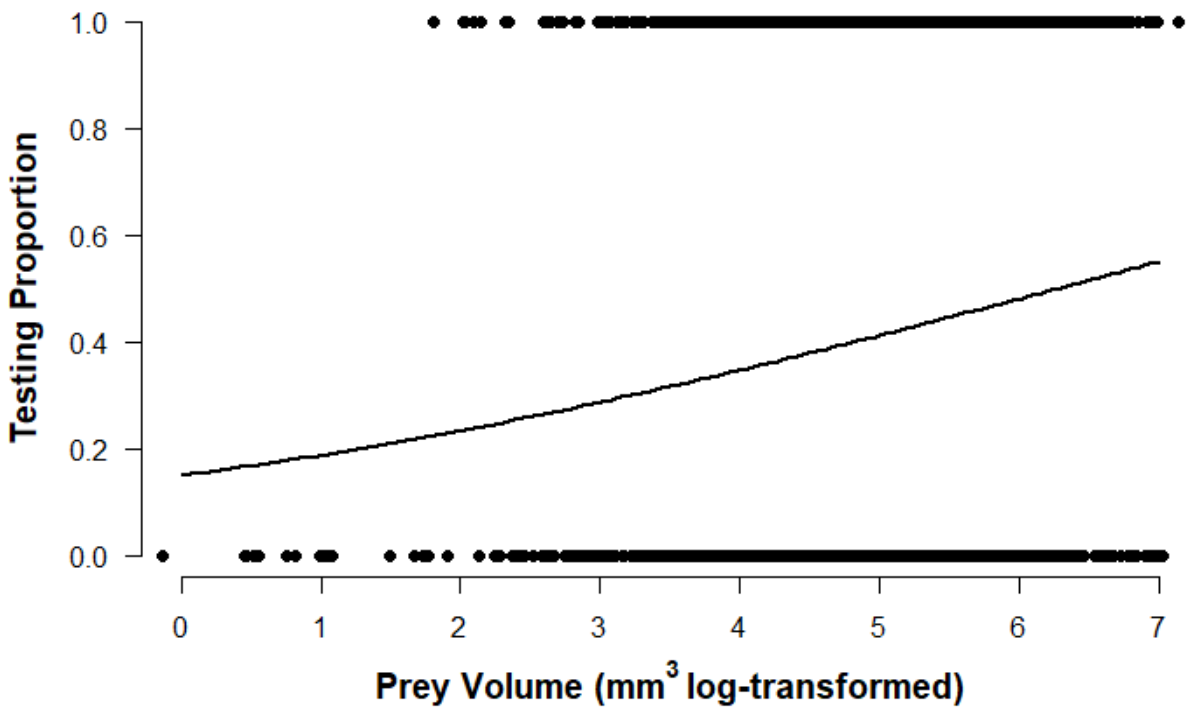


**Figure 4.3.** The effect of prey volume (log-transformed) on testing in the early nestling stage (0-4 d old) of mountain bluebirds. The points are either yes or no (1 or 0). The black curve shows the positive relationship between prey volume and testing proportion. There were 63 boxes filmed at the early nestling stage.

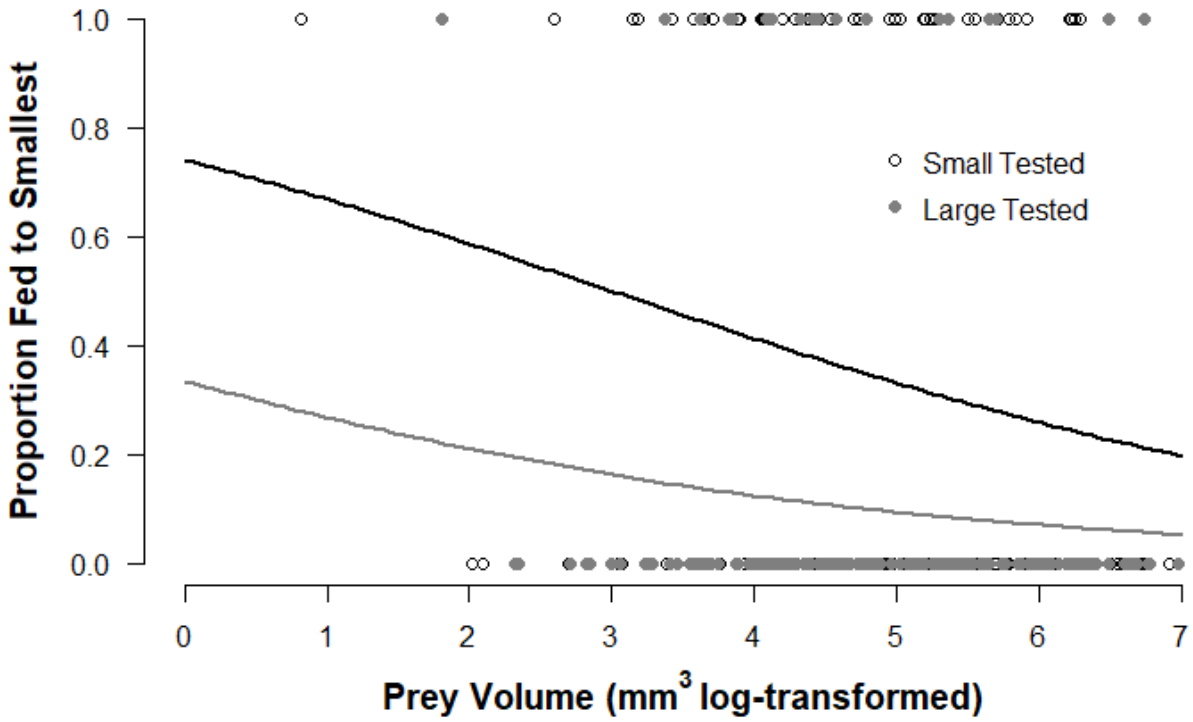


**Figure 4.4.** The effect of prey volume (log-transformed) on feeding the smallest mountain bluebird nestling after either the smallest or a larger nestling was tested first during the early nestling stage (0-4 d old). The points are either yes or no (1 or 0). The black curve shows the relationship when the smallest nestling was tested first, and the grey curve shows the relationship when a larger nestling was tested first. There were 40 boxes filmed at the early nestling stage with a marked smallest nestling.

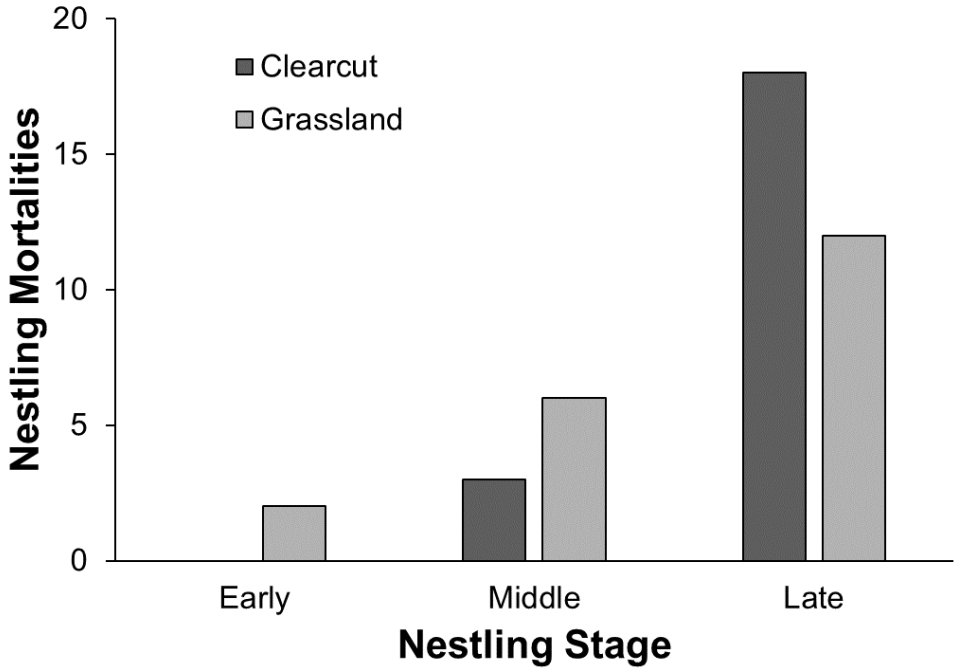


**Figure 4.5.** The relative distribution of bluebird nestling mortalities at each nestling stage (early: 0-4 d old, middle: 5-11 d old, late: $\geq$ 12 d old) in clearcut and grassland habitats in central British Columbia. Nest that failed completely because of depredation or abandonment are excluded. Total sample size was 23 nestlings that died in grasslands and 21 in clearcuts. Three nestlings from a grassland box were not included in the graph because I could not determine if they died during the middle or late nestling stage.

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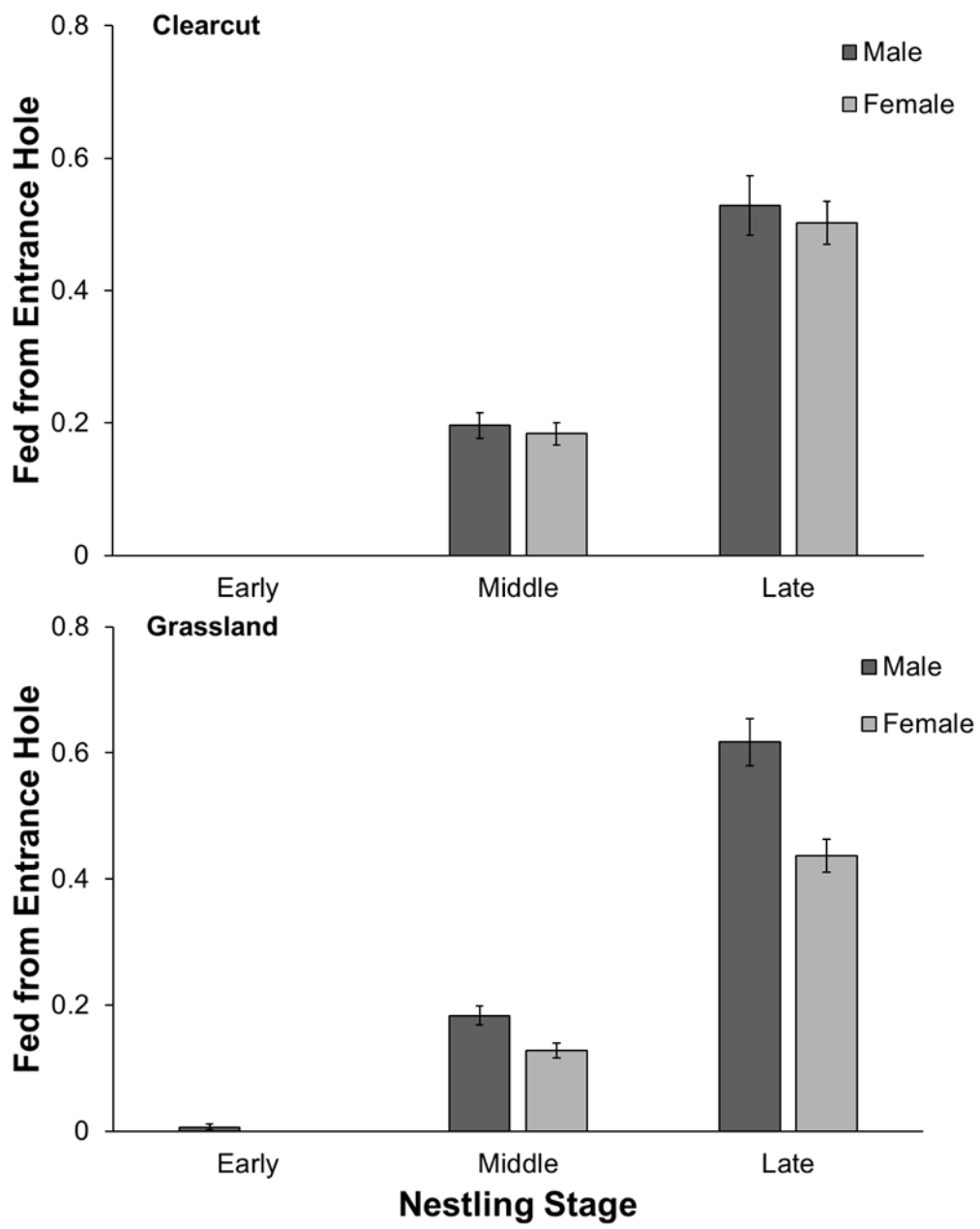


**Figure 4.6.** The average proportion ± SE of feeding events done from the entrance hole by mountain bluebirds in each nestling stage (early: 0-4 d old, middle: 5-11 d old, late: ≥ 12 d old) separated by habitat. The number of boxes with filming data for clearcuts was 37 for early, 40 for middle, and 12 for the late nestling stage. The number of boxes with filming data for grasslands was 26 for early, 35 for middle, and 16 for the late nestling stage.

# CHAPTER 5: GENERAL DISCUSSION

## 5.1 Overview

In this study, my first objective was to determine if mountain bluebirds were negatively affected by settling in clearcut habitats rather than their natural grassland habitat, focussing on the effects of prey quality and quantity. In Chapter 2, I found that adults in clearcuts were bringing larger food items than adults in grasslands, but that those prey items in clearcuts were of higher quality (larvae and spiders), which contradicted my prediction. However, adults in clearcuts had a lower delivery rate, negatively affecting the mass of their nestlings. This indicates that prey availability may be lower in clearcuts compared to grasslands.

In Chapter 3, I investigated whether clearcut habitats are an ecological trap for mountain bluebirds regarding prey availability. I found that adults were settling in both clearcuts and grasslands equally, possibly earlier in clearcuts. In general, early reproductive parameters (e.g. laying date) were similar between the females in both habitats, but females in clearcuts had a lower body condition than females in grasslands and abandoned broods more often in harsh weather events. Perhaps they had trouble finding enough food for themselves and their nestlings during the incubation and nestling periods. Regarding reproductive output, clearcuts produced a similar number of fledglings as grasslands (although fewer eggs in clearcuts reached fledging), but these fledglings in clearcuts were lower quality. Hence, clearcut habitats are an ecological trap if the lower quality of the nestlings reduces their survival post-fledging. However, this pattern was not as extreme as I predicted, so mountain bluebird populations may not decline greatly if they settle in this habitat.

The other main objective, covered in Chapter 4, was to test nestling gape size as a mechanism that constrains parents' provisioning ability, and therefore causes premature death of the youngest nestling in an asynchronous brood. Although I found that testing of nestling gapes was more frequent with large prey items, increased testing in younger nestlings did not affect

fledging success. Although prey types and volumes differed between clearcuts and grasslands, testing and the results of testing did not overall, so the prediction that there would be higher mortality rates for the youngest nestling in clearcut habitats was not supported. Mountain bluebirds may not have a high enough degree of asynchrony for testing and enough larger prey items to be a problem in general or to amplify the differences in nestling quality between the two habitats.

### 5.2 Future Research Directions and Conservation Notes

My research offers a preliminary overview of how the physical structure and vegetation in clearcuts versus grasslands in British Columbia might affect the reproductive success of insectivorous passerines that settle in clearcuts. Grassland bird populations have been decreasing for over 40 years (North American Bird Conservation Initiative Canada 2012). My results suggest that clearcuts might be able to sustain viable populations of some species adapted to grassland habitats, although productivity might be slightly lower in clearcuts. However, the fitness costs of using clearcuts may generally be higher than my study indicated because predation rates in my sites were lower than those reported in other studies. Therefore, there should be studies determining whether certain types of clearcuts (e.g. forest type, location) are more likely to be severe ecological traps as a result of nest predation.

Mountain bluebirds are cavity nesters that foraged mainly on insects on the ground, but it is important to see whether clearcuts might be ecological traps for other species with different nest or diet requirements. Tree swallows, for example, are another secondary cavity nester which are abundant in both habitat types, but which forage aerially on a different insect community. Similar studies could be done on arboreal or ground nesting insectivorous birds, but the nests of these species may be more challenging to find. However, not all grassland birds are insectivores, and the differences in vegetation and habitat structure could affect the food availability of more granivorous grassland birds.

My findings suggest that mountain bluebirds use different prey types and sizes in the two habitats, but I did not study whether they were choosing those prey items, or those prey items were the only prey items available. There needs to be a more comprehensive survey of invertebrate prey abundance in these two habitats to answer this question. Along with these surveys, there should be observational studies on hunting success and behaviours used in the two habitats in relation to perches and vegetation density. Also, there needs to be studies on post-

fledgling survival to determine if the lighter fledglings in clearcuts have lower survival rates compared to fledglings in grasslands.

In sum, my data suggest that clearcut habitat in central British Columbia might be a weak ecological trap, but they are not necessarily sink habitats and might offer alternative breeding habitat for mountain bluebirds. According to Stuart-Smith and Hayes (2003), increased residual tree density does not increase overall predation risk in clearcuts found in montane forests in southeastern British Columbia. Thus, bluebirds might benefit if the residual tree density left by loggers was enough for a high natural cavity abundance or nestboxes were placed in the clearcuts (away from the forest edge) if few grassland habitats were available. Although clearcuts produced nestlings of lower quality, the alternative to not settling in clearcuts may be that these mountain bluebirds could not reproduce at all. Therefore, clearcuts may partially mitigate any reductions to mountain bluebird populations caused by loss of grazed and native grasslands.

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## APPENDIX 1

**Table A1.1.** The proportion of ground cover type within 1 $m^2$ plots near each nestbox of mountain bluebirds. At each box, the average cover based on two plots was calculated and shown are the overall averages from 44 clearcut boxes and 52 grassland boxes. "Other debris" refers to lichen and dead plants. In each habitat, the 5 most common plant groups (not including grass) are in bold.

| Ground cover Type | Clearcuts | Grasslands |
|---|---|---|
| Bare Ground | 0.08 ± 0.01 | 0.18 ± 0.02 |
| Woody Debris | 0.13 ± 0.01 | 0.003 ± 0.001 |
| Grass | 0.16 ± 0.01 | 0.34 ± 0.02 |
| Other Debris | 0.24 ± 0.01 | 0.26 ± 0.02 |
| Asteraceae | **0.05 ± 0.01** | **0.08 ± 0.01** |
| Caryophyllaceae | 0.004 ± 0.001 | 0.003 ± 0.002 |
| Cornaceae | 0.005 ± 0.002 | 0 |
| Ericaceae | **0.05 ± 0.01** | 0.0003 ± 0.003 |
| Fabaceae | **0.06 ± 0.01** | **0.07 ± 0.01** |
| Geraniaceae | 0.002 ± 0.002 | 0.003 ± 0.002 |
| Lamiaceae | 0 | **0.01 ± 0.002** |
| Liliaceae | 0.01 ± 0.001 | 0 |
| Onagraceae | **0.03 ± 0.004** | 0 |
| Pinaceae | 0.01 ± 0.002 | 0 |
| Rosaceae | **0.1 ± 0.01** | **0.02 ± 0.004** |
| Rubiaceae | 0.02 ± 0.003 | **0.01 ± 0.002** |
| Salicaceae | 0.01 ± 0.002 | 0.001 ± 0.0005 |
| Other Plants | 0.02 ± 0.003 | 0.02 ± 0.003 |

## APPENDIX 2

**Table A2.1.** The percentage of all prey types that were fed to nestlings in clearcuts and grasslands. Cicadas were separated from Hemiptera because their bodies were relatively large and bulky. Unknown refers to (usually small), unidentifiable prey items or cases where parents brought multiple items that could not be distinguished. There were 2205 prey items brought in clearcuts and 2662 prey items brought in grasslands. Prey types are roughly ordered in decreasing abundance.

| Prey Type | Clearcuts | Grasslands |
|---|---|---|
| Larva | 40.54% | 28.21% |
| Spider | 26.44% | 15.18% |
| Coleoptera | 9.84% | 25.21% |
| Unknown | 6.53% | 11.46% |
| Orthoptera | 5.49% | 6.31% |
| Hymenoptera | 4.63% | 4.40% |
| Lepidoptera | 3.40% | 2.82% |
| Diptera | 1.77% | 2.52% |
| Odonata | 0.63% | 1.54% |
| Cicada | 0.18% | 1.43% |
| Ephemeroptera | 0.09% | 0.41% |
| Trichoptera | 0.09% | 0.3% |
| Annelida | 0.27% | 0.04% |
| Hemiptera | 0.09% | 0.04% |
| Neuroptera | 0% | 0.08% |
| Myriapoda | 0% | 0.04% |
| Plecoptera | 0% | 0.04% |